UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PERSONNALITÉ,
STRATÉGIES D'APPROVISIONNEMENT ET D'APPARIEMENT
CHEZ LES DIAMANTS MANDARINS (*TAENIOPYGIA GUTTATA*)

MÉMOIRE DE THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN BIOLOGIE

PAR

MORGAN DAVID

NOVEMBRE 2011

TABLES DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

En biologie évolutive, la variation phénotypique a longtemps été réduite au substrat sur lequel agissait la sélection naturelle. Toutefois, la constance intra-individuelle et le maintien intra-populationnel de certains comportements conduisirent au milieu des années 90 au développement du concept de personnalité animale, basé sur la caractérisation de traits tels que la néophobie, l'agressivité, les tendances exploratoires ou la prise de risque. De nombreuses études montrent que la personnalité est soumise à la sélection naturelle et est reliée à certaines stratégies biodémographiques, telles que la dispersion ou le comportement anti-prédateur.

Les liens entre la personnalité animale et les stratégies d'appariement et d'approvisionnement, deux composantes fondamentales de la vie des organismes, ont pourtant été négligés jusqu'ici. Nous nous sommes donc attachés au cours de cette thèse à déterminer l'influence de la personnalité sur certains comportements sexuels et alimentaires à l'aide d'un organisme modèle en écologie comportementale : le Diamant mandarin (*Taeniopygia guttata*). Puis, à l'inverse, nous avons souligné le rôle des sélections naturelle et sexuelle dans le maintien des variations de personnalité.

Nos résultats indiquent que certains traits de personnalité mesurés sont inter-corrélés au niveau de notre population captive d'oiseaux, définissant un syndrome comportemental. De plus, la personnalité prédit de manière différentielle le succès d'approvisionnement entre les contextes de compétition par exploitation et par interférence. Ainsi, les individus proactifs sont dominants lors d'épisodes de compétition par interférence mais souffrent d'un plus faible succès d'approvisionnement lors de jeux producteur-chapardeur. Ces résultats soulèvent la possibilité que la sélection naturelle favorise différentes personnalités dans différents contextes, offrant un mécanisme d'explication du maintien des variations intra-populationnelles de personnalité. De plus, ils suggèrent que la personnalité contraint l'optimalité des comportements à travers les situations. Enfin, dans un contexte de choix du partenaire, nous avons montré que la personnalité des femelles utilisées dans des tests de préférence par association influence les mesures de la sélectivité, des scores de préférence et de leur répétabilité.

L'étude conjointe de la personnalité animale et des stratégies d'appariement et d'approvisionnement constitue ainsi une voie prometteuse dans l'explication du maintien des variations de personnalité par sélections naturelle et sexuelle, ainsi que dans l'étude de l'influence de la personnalité sur les stratégies biodémographiques des organismes en contextes alimentaire et sexuel.

mots-clés : personnalité, syndromes comportementaux, *Taeniopygia guttata*, compétition alimentaire, choix du partenaire, sélection sexuelle, approvisionnement social, jeu producteur-chapardeur

INTRODUCTION

1.1. UNE HISTOIRE DE LA VARIATION

La variation morphologique ou comportementale caractérisant les individus d'une même population est considérée comme le substrat de l'évolution par sélection naturelle. Le processus de sélection naturelle est en effet assimilable à un tri différentiel des variants au cours d'une génération. Les individus possédant les caractéristiques morphologiques ou comportementales conférant la meilleure capacité à survivre et se reproduire dans l'environnement sont logiquement ceux qui laissent le plus de descendants. Si le caractère possède un certain degré d'héritabilité, ces mêmes individus contribuent donc plus que les autres membres de la population à sa composition génétique à la génération suivante. Cette nouvelle composition génétique de la population se traduit au plan phénotypique par un déplacement de la valeur moyenne du trait et/ou une modification de sa variance.

Si l'éthologie n'a que peu pris en considération les variants dans la description des comportements-types spécifiques pour se concentrer sur les différences entre espèces (Cézilly 2005), l'écologie comportementale s'est immédiatement intéressée à la variation intra-spécifique et à l'optimalité des comportements. L'émergence de cette jeune discipline au cours des années 70 offrit un paradigme et un cadre d'étude du comportement animal intégré à une vision évolutive (Cézilly 2005). L'écologie comportementale proposa ainsi d'envisager l'évolution des comportements par le succès différentiel et la sélection des variants au sein des populations. La question de la variation intra-populationnelle se plaça donc au centre des problèmes envisagés par cette discipline. Par exemple, la théorie de la sélection sexuelle prédit que la variance génétique à la base des ornements des mâles d'une population devrait s'éroder au fil des générations à mesure que les femelles expriment leur préférence et choisissent comme partenaire les individus possédant de « bons gènes » (en termes de survie, de croissance ou de résistance aux pathogènes…). Comme tous les mâles devraient ainsi

en quelques générations posséder les mêmes « bons gènes » et être de qualité similaire du point de vue des femelles, les pressions de sélection agissant sur la préférence de ces dernières devraient diminuer à tel point que les femelles n'expriment plus aucune préférence. Or, les exemples de variations de préférence et d'autres composantes du choix du partenaire comme les tactiques d'échantillonnage des partenaires potentiels abreuvent de manière récurrente la littérature (Jennions & Petrie 1997 ; Brooks & Endler 2001 ; Rios-Cardenas *et al.* 2007). Ce « paradoxe du lek » illustre un de ces défis de l'écologie comportementale en questionnant la place de la variation au sein du processus de sélection. Cet exemple illustre le conflit inhérent à l'écologie comportementale entre la variation comme substrat de la sélection et la variation comme résultat adaptatif potentiel de la sélection.

Si la variation interindividuelle a longtemps été appréciée comme le substrat sur lequel la sélection agit, peu de considération a été donné à l'hypothèse de la variation comme résultat de la sélection naturelle (Wilson 1998). L'explication du maintien adaptatif de la variation au sein des populations est ainsi une source d'investigation récente en biologie évolutive (Wilson 1998). La prise en compte de la variation intra-populationnelle comme conséquence adaptative potentielle de la sélection, et plus globalement, l'intérêt pour les différences interindividuelles continues (au-delà des exemples classiques discrets de la théorie des jeux) émergea progressivement au cours des années 90 en écologie comportementale (Verbeek *et al.* 1994 ; Wilson *et al.* 1994 ; Wilson 1998 ; figure 1.1.). L'impulsion vint ainsi des observations familières que les individus d'une même espèce diffèrent dans leurs réactions comportementales face à certaines situations, ce qui définit leur personnalité. Les premières études se sont ainsi attachées à décrire les variations observées des tendances téméraires, exploratoires, agressives, ou encore de prise de risque (Verbeek *et al.* 1994 ; Wilson *et al.* 1994), et à proposer des *scénarii* évolutifs responsables du maintien à la fois de la variation intra-populationnelle, mais également de la constance intra-individuelle des traits étudiés (Coleman & Wilson 1998 ; Wilson 1998). Le concept de personnalité décrit alors comme des tendances

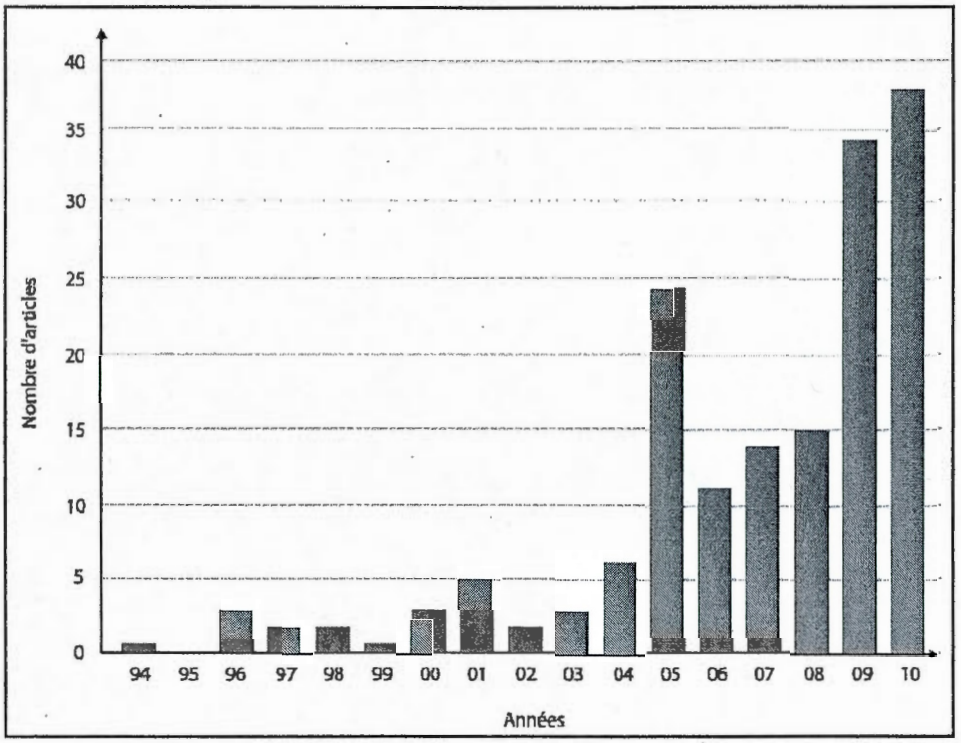

Figure 1.1. Nombre d'articles publiés de 1994 à 2010 contenant dans le titre, les mots-clés ou le résumé les termes « *behavioural syndrome* » (orthographes britannique et américaine), « *boldness* », « *coping style* », « *personality* » ou « *temperament* ». Les journaux analysés sont « *Animal Behaviour* », « *Behavioral Ecology* », « *Behavioral Ecology and Sociobiology* », « *Behaviour* », « *Behavioural Processes* » et « *Ethology* ».

individuelles intrinsèques et stables ce qui auparavant était considéré comme de la variance résiduelle autour d'une moyenne populationnelle adaptative.

1.2. LE CONCEPT DE PERSONNALITÉ ANIMALE

1.2.1. DÉFINITION

La personnalité humaine se définit comme des patterns comportementaux individuels distinctifs, constants à travers le temps et les situations (Pervin & John 1997). Les

psychologues utilisent classiquement des évaluations comportementales introspectives ou effectuées par des tiers, regroupées par la suite en grandes catégories de personnalité. Les cinq dimensions du « *Big Five* » (extraversion, caractère agréable, ouverture à l'expérience, stabilité émotionnelle, caractère consciencieux) représentent la méthode d'évaluation de la personnalité la plus connue (Rammstedt & Schupp 2008). La personnalité au cours de la vie humaine semble ainsi montrer une certaine constance, mais dépendante de la dimension prise en compte (Soldz & Vaillant 1999 ; Srivastava *et al.* 2003).

Si l'étude de la personnalité animale a pu se parer d'un avant-goût anthropomorphique, il est important de rappeler que son étude, si elle s'est basée sur les travaux conduits chez l'humain et leurs terminologies, n'en possède pas moins une histoire propre et une originalité (Gosling 1998). Toutefois, avant d'être abordée dans un cadre évolutif, la personnalité animale était caractérisée *via* les tendances comportementales originellement quantifiée chez l'humain, telles que la curiosité ou l'impulsivité (voir Gosling 1998, 2001 pour des synthèses). Le concept actuel de personnalité animale est, comme pour la personnalité humaine, basé sur la caractérisation intra-populationnelle de la variation comportementale entre individus (Bell 2007). La personnalité animale est ainsi définie comme les tendances intrinsèques émotionnelles affectant les réponses comportementales d'un organisme dans différents contextes, de manière constante au cours du temps. Cinq grandes catégories de personnalité ont récemment été proposées (Réale *et al.* 2007) : 1) l'axe timidité-témérité, désignant les réactions individuelles dans des situations risquées, mais pas nouvelles ; 2) l'axe exploration-évitement, qualifiant la réaction dans une situation nouvelle ; 3) l'activité, correspondant au niveau général d'activité d'un animal ; 4) l'agressivité, désignant les réactions agonistiques envers les congénères ; et 5) la sociabilité, correspondant à la réaction face à la présence et à l'absence de congénères, les individus sociables recherchant particulièrement leur présence alors que les asociaux la fuient.

De nombreux protocoles expérimentaux ont ainsi été mis en place à la fois en captivité et *in natura* afin d'évaluer les différents traits de personnalité. Le test de la distance minimale de fuite est utilisé dans la nature et sert à quantifier la témérité des animaux par la distance maximale accordée par un individu entre lui-même et un expérimentateur s'en approchant à vitesse régulière (Garamszegi *et al.* 2008 ; Møller *et al.* 2008). Les tests d'exploration et de nouvel objet servent à mesurer la réaction d'individus face à la nouveauté. Par exemple, lors du test de nouvel objet, un item original, inconnu de l'animal, est introduit dans sa cage de maintien, en général près d'une mangeoire. Le temps de latence avant d'aller s'alimenter, de parcourir l'objet, ou le temps passé à proximité, sont considérés comme des mesures d'exploration/d'évitement de la nouveauté. De même, le nombre de mouvements effectués à l'intérieur d'un dispositif d'exploration (figure 1.2.) ou le temps mis pour le parcourir entièrement permettent d'attribuer des scores d'exploration face à la nouveauté (Dingemanse *et al.* 2002, 2007). La témérité des individus peut être évaluée *via* la mesure du comportement de prise de risque, qui consiste souvent à calculer le temps de retour à une activité normale après une importante perturbation (van Oers *et al.* 2004) ou après présentation d'un prédateur réel ou factice (Quinn & Cresswell 2005 ; Reaney & Backwell 2007). Par exemple, les animaux téméraires retournent rapidement s'approvisionner à la mangeoire après y avoir été dérangés, alors que les plus craintifs mettent plus de temps à reprendre leur activité. Les tests d'agression consistent classiquement à placer un intrus, factice ou réel, en général un congénère, sur le territoire de l'individu focal et de quantifier le nombre d'attaques ou le temps de latence avant la première attaque (Duckworth 2006). Le test de la réaction face à son image dans le miroir est aussi utilisé pour quantifier l'agressivité face à un

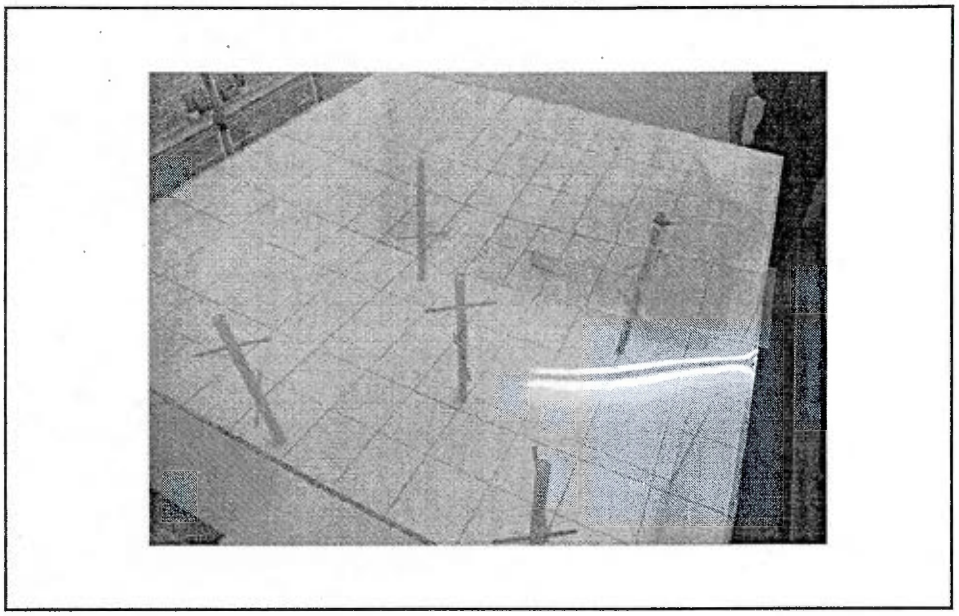

Figure 1.2. Dispositif expérimental d'évaluation des tendances exploratoires (vue de ¾).

congénère virtuel (Dochtermann & Jenkins 2007 ; Boon *et al.* 2007 ; Schuett 2008). Enfin, la sociabilité peut être évaluée à partir du temps passé dans un habitat avec ou sans congénères, ou avec ou sans signes de leur présence (Cote *et al.* 2008).

Toutefois, d'autres traits de personnalité ont déjà été définis dans la littérature, comme l'obstination, ou persévérance, ou la sélectivité (Sih & Bell 2008). La catégorisation de Réale *et al.* (2007) procure l'avantage d'éviter la redondance entre des traits de même nature, alors que la riche terminologie existante, parfois utilisée à mauvais escient, amène à une certaine confusion quant aux traits réellement mesurés. Ainsi la mesure de la réaction d'un animal face à un nouvel objet peut-elle être qualifiée de test de témérité (axe 1 de Réale *et al.* 2007) alors qu'il s'agit d'un test effectué face à une situation nouvelle (axe 2). Encore, le comportement exploratoire d'un animal dans un nouvel environnement se trouve appartenir à la fois à la catégorie 2 (exploration et évitement) et à la 3 (activité). Ainsi, différents tests de

personnalité effectués sur les mêmes individus peuvent en réalité correspondre à différentes manières de quantifier le même trait, ce qui, malgré le caractère fortuit de l'opération, n'est pas inintéressant en soi. Par exemple, le test de nouvel objet et le test d'exploration d'un nouvel environnement sont deux techniques permettant d'évaluer les tendances exploratoires et d'évitement (axe 2). L'évaluation d'un trait de personnalité à travers différents tests peut ainsi permettre d'évaluer la dépendance de la personnalité au contexte. Si, au niveau de l'échantillon d'étude, les réactions des individus face au nouvel objet ne sont pas liées à leurs réactions face au nouvel environnement, alors le trait de personnalité d'exploration/évitement peut être considéré comme dépendant du contexte au sein duquel il est évalué. On peut imaginer que, la constance des traits de personnalité représentant un des principes théoriques de ce concept, les auteurs d'études expérimentales ont pu être amenés à démultiplier l'identification et la qualification de différents traits de personnalité, par exemple parce que des traits de même nature n'étaient pas constants à travers différents types de mesure. On peut ainsi imaginer que la dépendance au contexte des traits de personnalité ait été sous-estimée et ait entrainé l'identification d'un nombre élevé de traits pourtant de nature semblable. Evidemment, la résolution de cette question passe par celle de l'identification de la nature même des traits de personnalité. En ce sens, la découverte de leurs causes proximales génétiques ou physiologiques (Bergmüller 2010) apporte un moyen de catégorisation utile, et *in fine*, des réponses au conflit entre constance et dépendance au contexte des traits de personnalité. Ces considérations rejoignent la problématique des syndromes comportementaux et des corrélations fluctuantes entre traits (voir partie 1.2.2.4. ; Bell & Sih 2007).

Le nombre de définitions différentes données au concept de la personnalité animale équivaut pratiquement au nombre d'articles théoriques publiés sur le sujet. Ainsi, aucun consensus n'a aujourd'hui été trouvé sur la définition de la personnalité animale. Parfois, la personnalité est assimilée aux différences inter-individuelles, quelle que soit leur nature. N'importe quel comportement, variable au niveau de la

population et constant intra-individuellement est alors appelé personnalité. Cette formulation suscite toutefois des interrogations quant à la nécessité d'utiliser une nouvelle terminologie pour qualifier les différences inter-individuelles. En effet, cette variation intra-populationnelle est couramment étudiée, notamment en écologie évolutive, sans faire référence au terme personnalité (Bolnick *et al.* 2003, 2009).

De cette inclusion de la personnalité dans le contexte plus général des différences inter-individuelles résulte un rejet logique du caractère émotionnel des réactions comportementales influencées par la personnalité. Les émotions peuvent être définies comme des états psychologiques et physiologiques complexes permettant à un organisme d'évaluer la désirabilité des évènements survenant dans son environnement (Dolan 2002). Il apparaît pourtant évident que les réactions comportementales étudiées au moment de la formulation du concept « évolutif » actuel de personnalité trouvaient leurs origines dans l'expression d'émotions. En effet, les premières études de personnalité animale conduites par des écologistes du comportement portaient sur des réactions émotionnelles comme la néophobie, l'exploration ou la prise de risque (Verbeek *et al.* 1994 ; Godin & Dugatkin 1996 ; Coleman & Wilson 1998). Le terme « personnalité », tel qu'il est utilisé en écologie comportementale, est donc issu de la caractérisation de réactions émotionnelles, et la généralisation sémantique à toutes les différences inter-individuelles comportementales n'est qu'une extension de son utilisation originelle. L'utilisation du qualificatif « émotionnel » pour définir la personnalité serait donc nécessaire pour justifier l'utilisation de cette terminologie sans la rendre réductible à l'utilisation des termes « différences inter-individuelles ». Historiquement donc, la personnalité animale est liée au caractère émotionnel des réactions comportementales et ne peut pas se confondre avec toutes sortes de différences inter-individuelles. Toutefois, au niveau mécanistique et fonctionnel, personnalité et différences inter-individuelles partagent les mêmes questions et enjeux théoriques, à savoir l'explication évolutive de la variation intra-populationnelle et intra-individuelle (voir partie 1.2.2.3.). En ce sens, les questions évolutives relatives à la personnalité peuvent être intégrées à celle

des différences inter-individuelles, ce qui explique que certains biologistes du comportement ne trouvent pas nécessaire, d'effectuer la distinction entre les deux.

1.2.2 INTÉRÊTS DU CONCEPT

Le nombre d'articles produits sur le thème de la personnalité animale, comme montré dans la figure 1.1., connait une véritable croissance exponentielle depuis le milieu des années 90. Plusieurs raisons peuvent expliquer ce succès. Nous en détaillerons trois ici : l'ubiquité de la personnalité à travers le règne animal, ses relations avec différents traits et stratégies biodémographiques (ou traits d'histoire de vie), et les défis théoriques posés à l'évolution des comportements en général.

1.2.2.1. Ubiquité à travers le règne animal

L'observation que les animaux d'une même population diffèrent entre eux dans leur comportement et leur personnalité propre a toujours paru évident aux personnes profitant de contacts étroits et prolongés avec les animaux. Ainsi, les propriétaires d'animaux domestiques ou les techniciens animaliers de zoos ont depuis longtemps eu l'occasion d'observer et de caractériser subjectivement cette variation inter-individuelle à l'aide d'une terminologie anthropomorphique (Gosling 2001), avant que l'écologie comportementale ne s'y intéresse et tente d'organiser une classification méthodique des réactions observées (Réale *et al.* 2007). Les caractères curieux, impulsif, imaginatif ou irritable ont par exemple été étudiés chez les hyènes tachetées *Crocuta crocuta* (Gosling 1998), les caractères opportuniste ou confiant chez les macaques à face rouge *Macaca arctoides* (Figueredo *et al.* 1995). Suivant la catégorisation de Réale *et al.* (2007), les variations entre individus ont été caractérisées chez une vaste gamme de groupes, des mollusques (Sinn *et al.* 2006) aux mammifères (Réale *et al.* 2000 ; Martin & Réale 2008 ; Michelena *et al.* 2009), en passant par les crustacés (Reaney & Backwell 2007), les arachnides (Johnson &

Sih 2007), les insectes (Kortet & Hedrick 2007); les poissons (Àlvarez & Bell 2007 ; Brown *et al.* 2007) et les oiseaux (Dingemanse *et al.* 2002 ; Tobler & Sandell 2007). Si la majorité des études en écologie comportementale portaient récemment encore sur le modèle aviaire (Owens 2006), il semble que les études sur la personnalité soient aujourd'hui plus également distribuées dans le règne animal, même si les oiseaux, et en particulier la mésange charbonnière (*Parus major*), furent les premiers organismes modèles de l'approche évolutive de la personnalité (Verbeek *et al.* 1994).

La présence de variation sur les traits de personnalité chez une large gamme d'espèces facilite ainsi son étude en la rendant accessible à de nombreux organismes modèles. De plus, cette ubiquité stimule les comparaisons inter-spécifiques permettant d'appréhender l'évolution de la personnalité à travers ses différences et similarités fonctionnelles entre espèces.

1.2.2.2. Corrélations à d'autres traits

L'intérêt de la quantification de la personnalité chez une espèce réside également dans les corrélations avec d'autres traits ou des stratégies biodémographiques. Les réactions comportementales liées à la personnalité ne sont pas indépendantes d'autres comportements traditionnellement étudiés. La mise en relation d'une stratégie biodémographique à un certain type de personnalité permet ainsi de pouvoir prédire les futures décisions des organismes liées à un comportement donné en déterminant leur personnalité en environnement contrôlé (Jones & Godin 2010). De plus, ces corrélations incitent à déterminer leur cause, la raison de leur existence, et à envisager une vision plus intégrative du comportement des animaux en considérant que ces traits n'évoluent pas indépendamment les uns des autres (cet argument sera repris dans la partie 1.2.2.4.). De nombreux exemples empiriques permettent d'apprécier les liens existant entre personnalité et traits biodémographiques. Ainsi, l'éloignement post-natal *(post-natal dispersal)* a été relié aux tendances exploratoires dans un

nouvel environnement chez les mésanges charbonnières femelles (Dingemanse *et al.* 2003), et à la sociabilité chez le lézard *Lacerta vivipara* (Cote & Clobert 2007) et le poisson *Gambusia affinis* (Cote *et al.* 2010). Les individus effectuant le plus de mouvements dans le dispositif d'exploration ou se montrant plus asociaux s'éloignaient à plus longue distance de leur lieu de naissance ou étaient simplement plus susceptibles de s'en éloigner. Chez les mésanges de Gambel (*Poecile gambeli*), la dominance lors d'interactions agressives est liée aux tendances exploratoires dans un nouvel environnement mais pas face à un nouvel objet (Fox *et al.* 2009). Ainsi, les individus les moins actifs dans le nouvel environnement avaient plus de chance de devenir dominant par la suite face aux plus actifs. Une étude conduite à la fois sur des individus d'une population invasive et résidente de moineaux domestiques (*Passer domesticus*) a montré que les deux populations différaient dans la tendance à manger de la nourriture inconnue mais pas dans celle à s'alimenter près d'un objet inconnu (Martin II & Fitzgerald 2005). Les individus issus de la population invasive étaient plus enclins que ceux issus de la population résidente à s'approvisionner à partir de nourriture inconnue. Les auteurs en conclurent que les différences de personnalité en termes d'exploration/évitement peuvent prédire le succès des invasions biologiques et de l'expansion de populations existantes. Chez les bernaches nonettes (*Branta leucopsis*), les individus dirigeant le groupe de congénères sont les plus explorateurs lors du test de nouvel objet (Kurvers *et al.* 2009). Toutefois, aucune relation n'a été décelée avec d'autres traits comme la dominance, l'exploration d'un nouvel environnement ou l'activité intrinsèque. Enfin, chez les étourneaux sansonnets (*Sturnus vulgaris*), les individus les plus rapides à s'alimenter dans un environnement inconnu possèdent des meilleures performances d'apprentissage que les autres individus (Boogert *et al.* 2006). De même, chez les mésanges à tête noire (*Poecile atricapillus*), les individus les plus explorateurs se montrent plus rapides dans l'apprentissage d'une tache de discrimination acoustique que les individus peu explorateurs (Guillette *et al.* 2009). Toutes ces études suggèrent donc que la personnalité animale peut être utilisée pour prédire la variation existante sur certains

traits comportementaux et stratégies biodémographiques. De plus, cette abondante littérature invite à repenser l'évolution des comportements en incitant à considérer que chaque trait n'évolue certainement pas indépendamment mais en co-évolution au sein d'un ensemble adaptatif (cet argument sera repris dans la partie 1.2.2.4.).

1.2.2.3. Défis théoriques du concept

En plus d'une certaine ubiquité à travers le règne animal et de ses liens avec de nombreux autres traits, le concept de personnalité représente un défi théorique important face à la question de l'évolution des comportements, du principe d'optimalité et de la flexibilité comportementale. Ainsi, les deux caractéristiques principales du concept de personnalité, que sont la constance intra-individuelle et la variation intra-populationnelle, représentent précisément les points défiant la conception traditionnelle de l'évolution des comportements. En écologie comportementale, il est communément admis que le comportement des individus est flexible de manière à s'adapter de façon optimale aux différentes situations. A l'inverse des caractères morphologiques ou physiologiques dont la plasticité phénotypique permet d'engendrer de la variation adaptative sur une seule génération, la flexibilité comportementale est censée produire une réponse encore plus rapide permettant à l'individu de s'ajuster de manière optimale et réversible aux variations de l'environnement. Le principal bénéfice de la flexibilité comportementale résiderait ainsi dans la rapidité avec laquelle les individus répondent aux différentes pressions de sélection de l'environnement, *via* la cognition, dans la mesure où ces bénéfices dépassent les coûts associés à cette flexibilité (DeWitt *et al.* 1998) Pour toutes ces raisons, la constance intra-individuelle des traits de personnalité représente un défi à la vision classique de l'évolution des comportements. Par exemple, certaines proies devraient rester « timides » quel que soit le contexte lorsque le risque de prédation est accru et devenir plus « téméraires » lorsqu'il est réduit. Les tendances exploratoires et

néophobes devraient également être modulées en contexte d'approvisionnement en fonction de la rareté de la ressource et de la compétition entre individus, de sorte qu'une faible disponibilité en ressources ou une augmentation de la compétition encouragent les individus à augmenter l'étendue de leur recherche ou le type de nourriture collectée. Toutefois, les études s'intéressant à la constance des traits de personnalité à travers les contextes montrent que, même si l'intensité des comportements varie effectivement, l'ordre de rang entre les individus peut être maintenu de sorte que les organismes les plus téméraires dans le premier contexte le sont également dans le second (figure 1.3. ; Sih *et al.* 2003 ; Johnson & Sih 2007). Par exemple, pour les merles bleus de l'ouest (*Sialia mexicana*), les cavités leur permettant de nicher sont une ressource très limitante. Aussi, les mâles font preuve d'un certain niveau d'agressivité afin de défendre ces cavités face aux individus nicheurs d'autres espèces et d'empêcher d'autres mâles de la même espèce de venir copuler avec leur propre femelle. Duckworth (2006) a montré que les niveaux d'agressivité des mâles étaient constants à travers les contextes de défense du nid et de compétition entre mâles. Pourtant, les mâles les plus agressifs sont ceux dont le succès reproducteur se trouvait être le plus faible, car ils sont obligés de compromettre l'approvisionnement de la femelle couvant les œufs en investissant dans la défense des ressources. Cet élégant exemple illustre la constance des traits de personnalité à travers les contextes et le fait que ces corrélations inter-contextes puissent potentiellement empêcher les individus d'adopter un comportement optimal, compromettant ainsi leur aptitude phénotypique. D'autres exemples sont également disponibles chez d'autres espèces. Ainsi, une corrélation entre les niveaux d'activité et de prise de risque en présence et absence de signaux de prédateurs a été observée chez la salamandre *Ambystoma barbouri* (Sih *et al.* 2003). Chez une espèce d'arachnide (*Dolomedes triton*), Johnson & Sih (2007) ont observé que les indices de témérité étaient corrélés entre les contextes d'approvisionnement et de parade sexuelle. Toutefois, certaines études montrent également que des traits de personnalité tels que la témérité (Wilson & Stevens 2005), ou la relation entre

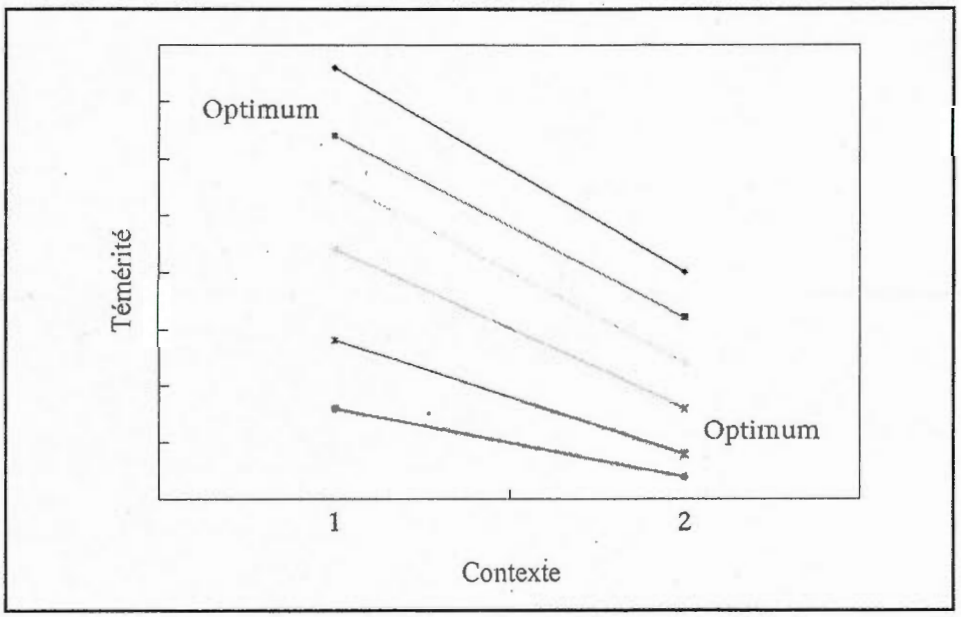

Figure 1.3. Illustration de la constance intra-populationnelle des traits de personnalité: si l'intensité de l'expression d'un trait peut varier entre les contextes de manière intra-individuelle, les rangs entre les individus sont conservés de sorte que les plus téméraires dans un contexte seront également les plus téméraires dans le second. Cette figure illustre la possibilité qu'une flexibilité limitée conduisent les individus à ne pas exprimer le comportement optimal dans chaque contexte (tiré de Johnson & Sih (2007).

exploration et dominance (Dingemanse & de Goede 2004) peuvent dépendre du contexte, ce qui prouve que les corrélations inter-contextes ne sont pas universelles et ne sont pas une condition *sine qua non* de l'existence des variations de personnalité. Enfin, ces études suggèrent que ces corrélations entre traits puissent être soumises à la sélection naturelle et être sélectionnées ou contre-sélectionnées selon les cas (voir partie 1.2.2.4.).

En plus de la constance intra-individuelle, la variation intra-populationnelle représente le second défi porté par le concept de personnalité, en partie pour les

raisons déjà invoquées plus haut. Ainsi, la répétabilité intra-individuelle des traits de personnalité implique logiquement une variation inter-individuelle. Une partie des problèmes posés par la constance intra-individuelle est donc également applicable à la variation inter-individuelle. Ainsi, comment expliquer que différents individus adoptent différents comportements dans une même situation alors que, *a priori*, un seul y est optimal (figure 1.3.) ? Cette problématique est d'autant plus pertinente et perceptible lorsque l'on s'intéresse à des traits de personnalité dont on suppose qu'ils sont soumis à de fortes pressions de sélection et influencent fortement l'aptitude phénotypique individuelle. Par exemple, on s'attendrait à ce que la témérité face aux prédateurs, illustrée par le comportement d'inspection du prédateur chez le guppy *Poecilia reticulata* (Godin & Dugatkin 1996), soit fortement contre-sélectionnée. Ainsi, la variation intra-populationnelle devrait se trouver réduite sous l'effet des sélections stabilisantes, voire directionnelles, pour ce type de trait de personnalité. Or une variation est couramment observée, alors qu'il semble qu'une seule valeur du comportement soit optimale dans une situation donnée. On ne s'attend donc pas à observer autant de variation qui en principe aurait du s'éroder sous l'effet de la sélection. Pour toutes ces raisons, la constance intra-individuelle et la variation intra-populationnelle représentent deux défis théoriques importants au principe d'optimalité, à l'évolution des comportements et de leur flexibilité.

1.2.2.4. Les syndromes comportementaux

La constance des traits de personnalité au cours du temps et entre différents contextes, associée à la diversité des techniques mises en œuvre afin de les quantifier, ont pu révéler la présence de corrélations multiples entre traits au niveau des populations. Ainsi, un « syndrome comportemental » se définit comme un ensemble de comportements corrélés au niveau de la population, pouvant refléter la constance comportementale individuelle à travers plusieurs situations (figure 1.4. ; Sih *et al.*

2004). Cette définition a l'intérêt de couvrir plusieurs cas d'études : par exemple, lorsqu'un trait de personnalité (*e.g.* la témérité) présente une constance au niveau individuel à travers différents contextes (*e.g.* approvisionnement, appariement...), ou quand différents traits de personnalité sont corrélés au niveau de la population. Le concept de syndrome comportemental est né avec le concept de personnalité, et des études sont très vite venues illustrer leurs similitudes et leur complémentarité (Brodin 2009 ; Wilson *et al.* 2010a). Ainsi, chez l'épinoche à trois épines, les comportements d'agression, d'activité, d'exploration d'un nouvel environnement, d'un environnement altéré, ou d'une nourriture inconnue sont tous inter-corrélés chez certaines populations (Dingemanse *et al.* 2007). Chez les Diamants mandarins (*Taeniopygia guttata*), les tendances exploratoires, évaluées en isolement ou en présence d'un congénère sont liées (Schuett & Dall 2009). L'étude conduite par Bell & Sih (2007) illustre à elle seule l'importance et les enjeux des corrélations comportementales intra-populationnelles. Ces auteurs ont utilisé l'épinoche à trois épines afin de déterminer l'influence de la prédation sur la présence d'un syndrome comportemental. Les comportements de témérité face à un prédateur et d'agressivité face à un congénère furent dans un premier temps quantifiés. Puis les épinoches furent placées dans des aquariums en conditions semi-naturelles pendant 24 heures en présence de prédateurs, en l'occurrence des truites arc-en-ciel (*Oncorhyncus mykiss*). Les épinoches survivantes furent ensuite récupérés et leurs traits de personnalité de nouveau testés. Les auteurs ne trouvèrent aucune relation entre les comportements individuels d'agression et de témérité avant l'expérience de prédation, alors qu'après, un syndrome comportemental défini par une corrélation positive entre agression et témérité fut mis en évidence chez les survivants. Ce syndrome fut révélé après l'épisode de prédation par la sélection positive des individus dont les deux traits étaient déjà dans le sens de la corrélation avant l'épisode de prédation, mais également du fait que certaines autres épinoches ont ajusté leur personnalité après l'épisode dans le sens de la corrélation. Il semble donc que la prédation ne soit pas seule responsable de l'établissement de ce syndrome, mais également que des

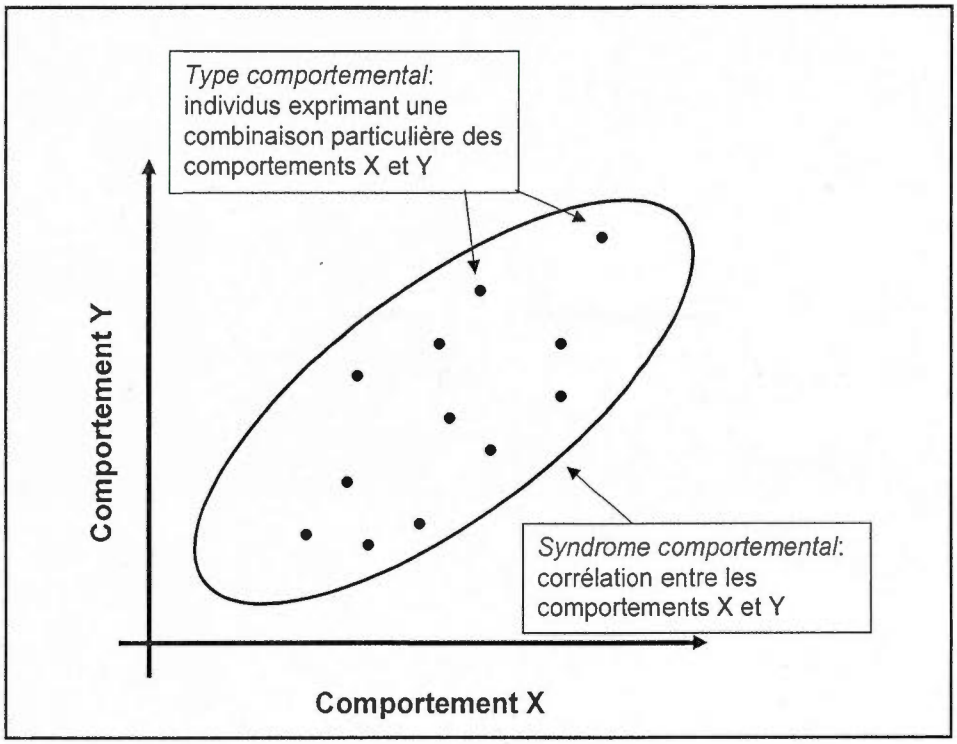

Figure 1.4. Graphique illustrant les notions de syndrome comportemental et de type comportemental. Chaque point représente un individu de la population (adapté de Bell (2007).

individus ajustent leurs comportements de manière adaptative suite à l'évènement de prédation. Les individus adoptant des niveaux d'agression et de témérité similaires (qu'ils soient faibles, intermédiaires ou élevés) encourraient ainsi un risque de prédation moins élevé. Cette étude illustre donc l'importance des corrélations comportementales dans la dynamique des populations et l'évolution des traits de personnalité et de leurs corrélations. La corrélation entre différents traits pourrait elle-même être l'objet de la sélection. Toutefois, la raison pour laquelle les corrélations elles-mêmes sont sélectionnées ou contre-sélectionnées reste inconnue et d'autres

études sont nécessaires afin de comprendre leur origine (Bell & Stamps 2004). Les comparaisons intra-populationnelles sont un point de départ permettant de comprendre quels facteurs écologiques modulent l'intensité des corrélations entre traits de personnalité. Ainsi, toujours chez la même espèce et dans le même contexte de prédation, Dingemanse *et al.* (2007) ont mis en évidence que le syndrome comportemental entre les traits d'activité, d'agressivité et d'exploration n'est présent que dans les populations soumises à la prédation.

Le concept des syndromes comportementaux apporte ainsi ses propres questions théoriques focalisées sur les corrélations entre comportements, au-delà de celles relatives à la personnalité énoncées auparavant. La présence de syndromes comportementaux invite à dépasser la vision d'une évolution adaptative indépendante de chaque trait dans un contexte précis et à adopter une vision intégrative considérant le comportement d'un individu comme irréductible à la somme de différents traits. Cette nouvelle vision offre ainsi de nouvelles perspectives quant à l'évolution des comportements. Du fait des corrélations entre traits, l'évolution d'un comportement est contrainte par l'évolution des autres comportements auxquels il est corrélé. Un individu ne pourra donc pas adopter n'importe quelle valeur d'un comportement x, en rapport à la valeur adoptée sur un comportement y qui lui est corrélé. La présence de syndromes comportementaux implique la présence de contraintes sur l'expression de certains comportements, par d'autres comportements. Les études sur les syndromes permettront de déterminer si ces corrélations sont adaptatives et contrebalancent les coûts associés à cette réduction de la flexibilité comportementale. L'intégration des contraintes comportementales découlant du concept des syndromes comportementaux offre à la fois des perspectives de réponse à des questions existantes en même temps qu'elle en pose de nouvelles. Les corrélations entre traits de personnalité possèdent ainsi le potentiel d'expliquer des comportements à première vue maladaptatifs, comme la témérité face aux prédateurs, par l'hypothèse des contraintes (Sih *et al.* 2004). Par exemple, le bénéfice de se comporter de manière téméraire en contexte de compétition pour des ressources alimentaires pourrait compenser le coût de se

montrer téméraires en présence de prédateurs. Enfin, la présence des syndromes comportementaux, mais aussi la mise en évidence d'un manque de flexibilité comportementale, portent atteinte à la théorie du pari phénotypique (*phenotypic gambit* en anglais), postulant que la sélection devrait être capable d'optimiser chacun des traits d'un individu de manière adaptative et de briser des contraintes telles que les corrélations entre traits. Pour reprendre l'exemple précédent, la sélection devrait pouvoir amener les individus d'une espèce donnée à s'ajuster aux conditions environnementales en réduisant la témérité en présence de prédateurs et en l'augmentant en contexte de compétition.

Pour conclure, les défis théoriques associés au concept des syndromes comportementaux sont évidemment indissociables de la question de la constance des traits de personnalité et de leur manque de flexibilité. Si les comportements étaient infiniment plastiques et si les individus pouvaient s'ajuster de manière adaptative aux différentes situations rencontrées, les syndromes ne pourraient plus être considérés comme un résultat potentiellement adaptatif issu de contraintes qui lui sont inhérentes, mais plutôt comme l'addition de comportements individuellement optimaux dans une situation donnée. Les syndromes en perdraient leur potentiel explicatif et leur intérêt théorique.

1.2.3. HYPOTHÈSES D'ÉVOLUTION DE LA PERSONNALITÉ

1.2.3.1. Personnalité et sélection naturelle

Le concept de personnalité se caractérise par une constance comportementale individuelle et de la variation intra-populationnelle. Une des principales questions associée à ce concept réside dans l'explication adaptative de cette variation. L'un des processus évolutifs capable de modifier la fréquence des variants au sein d'une population est la sélection naturelle (Endler 1986a). Ainsi, la variation couramment observée sur les traits de personnalité pourrait être maintenue par la sélection

naturelle. En effet, une multitude de données prouve aujourd'hui que la personnalité remplit les trois conditions fondamentales lui permettant d'évoluer par sélection naturelle (Endler 1986b ; Réale & Festa-Bianchet 2003 ; Quinn *et al.* 2009), à savoir : 1) l'existence d'une variation de personnalité entre les individus ; 2) l'existence d'une relation univoque entre cette variation et l'aptitude phénotypique des individus ; et 3) l'existence d'un certain degré d'héritabilité de la personnalité.

La variation inter-individuelle représente le cœur même du concept de personnalité. Toutes les études empiriques sont justement basées sur les tendances téméraires, exploratoires différant entre individus. Certaines études se sont attachées à établir la distribution de fréquence de ces tendances au sein de l'échantillon d'étude, par exemple chez les mésanges charbonnières (Verbeek *et al.* 1994), les Diamants mandarins (Schuett & Dall 2009), les mésanges de Gambel (Fox *et al.* 2009), ou une espèce de crabe *Uca mjoebergi* (Reaney & Backwell 2007). Il apparaît que ces distributions de fréquence ne sont jamais totalement normales ou bimodales, mais plutôt plates ou biaisées en faveur d'un extrême du *continuum*. Les distributions de fréquence des traits de personnalité ne montrent donc pas le profil-type d'un trait présentant de la variation aléatoire autour d'une moyenne adaptative (*i.e.* distribution normale, Wilson 1998), ou celui d'un trait soumis à une sélection diversifiante nette (*i.e.* distribution bimodale).

De nombreuses études montrent que les variations d'aptitude phénotypique individuelle co-varient avec la variation observée sur les traits de personnalité (Reaney & Backwell 2007 ; Réale *et al.* 2009 ; Wilson *et al.* 2010b). A l'aide d'une méta-analyse, Smith & Blumstein (2008) ont montré que la témérité avait globalement un effet positif sur le succès reproducteur, surtout chez les animaux captifs, alors qu'elle avait un effet négatif sur la survie. Alternativement, les tendances exploratoires et l'agressivité n'influencent que marginalement le succès reproducteur ou la survie. Au niveau spécifique, ces effets sont souvent plus marqués, et, de manière intéressante, parfois fluctuants à l'intérieur de la même espèce ou de la même population. Par exemple, dans une étude sur une population nord-américaine

d'écureuils roux (*Tamiasciurus hudsonicus*), l'agressivité des femelles prédit de manière fluctuante, mais significative à travers les années de suivi, la probabilité de survie de la progéniture (Boon *et al.* 2007). Certaines années, les femelles les plus agressives engendrent le plus de petits survivant à l'hiver, alors que pour d'autres années c'est le cas des femelles les moins agressives. De la même manière, une étude conduite sur trois années sur une population de mésanges charbonnières a déterminé que le taux de survie individuelle dépendait à la fois des tendances exploratoires, du sexe et de la disponibilité en nourriture pour l'année concernée (Dingemanse *et al.* 2004). Ainsi, la compétition pour la nourriture en hiver et pour les territoires au printemps pourraient être des facteurs modulant le succès différentiel des différentes personnalités au cours des années. Toutes ces études montrent donc que la variation observée sur les traits de personnalité est loin d'être neutre vis-à-vis de la sélection naturelle. La direction de la sélection est toutefois difficile à prédire au niveau spécifique du fait du peu de connaissances des facteurs liant personnalité et aptitude phénotypique.

Enfin, de nombreuses études ont révélé que les traits de personnalité possédaient un certain degré d'héritabilité, achevant, en plus des deux précédentes conditions, de les soumettre à la sélection naturelle. Les mésanges charbonnières ont constitué un modèle d'étude important dans l'estimation des coefficients d'héritabilité des traits de personnalité. Ainsi, les tendances exploratoires ont montré des coefficients d'héritabilité de 0,20 à 0,40 (Dingemanse *et al.* 2002), et jusqu'à 0,55 (Drent *et al.* 2003). Chez la même espèce, l'héritabilité de la témérité a été estimée à environ 0,20 (van Oers *et al.* 2004). Enfin, chez une espèce de seiche (*Euprymna tasmanica*), Sinn *et al.* (2006) ont estimé l'héritabilité de différentes facettes de la témérité dans une gamme de variation allant de 0,20 jusqu'à 0,80. Ces valeurs d'héritabilité sont ainsi moyennes voire supérieures à l'héritabilité moyenne observée des traits comportementaux (Stirling *et al.* 2002).

La sélection naturelle pouvant être un processus évolutif responsable du maintien de la variation sur les traits de personnalité, les différentes hypothèses évolutives proposées à l'épreuve de cette influence vont donc par la suite être présentées. L'effort sera ciblé sur les hypothèses adaptatives et co-évolutives, et sur les facteurs écologiques modulant la sélection sur la personnalité.

1.2.3.2. Le rôle de la sélection fréquence-dépendante

Au sein des populations d'animaux, les comportements n'évoluent évidemment pas seulement en fonction de l'environnement abiotique mais également en fonction des interactions inter-spécifiques, comme le risque de prédation ou les pressions parasitaires (Sorci & Cézilly 2005). A un niveau inférieur, le bénéfice que retire un individu donné en manifestant tel ou tel comportement peut dépendre du comportement adopté par ses congénères selon le processus de sélection fréquence-dépendante (Maynard-Smith 1982). Ainsi, la fréquence à laquelle un comportement est adopté par un individu, ou la fréquence d'individus jouant exclusivement une stratégie donnée dépend des comportements adoptés par les congénères de la population.

Wilson *et al.* (1994) ont proposé que la variation intra-populationnelle de personnalité ait pu évoluer par sélection fréquence-dépendante. Ces auteurs formulèrent un modèle verbal simple, basé sur l'exploitation d'une ressource, pour illustrer leur hypothèse. Deux types d'habitats distincts à l'origine inexploités sont ainsi considérés : l'un sûr et l'autre dangereux en termes d'exposition au risque de prédation. Lors de leurs colonisations, les individus d'une espèce donnée devraient s'installer dans l'habitat le plus sûr, jusqu'à ce que les coûts dus à la surpopulation dépassent les bénéfices de résider dans l'habitat sûr. Les nouveaux arrivants devraient alors s'installer dans l'habitat plus dangereux, où le rapport coûts/bénéfices entre densité de la population et risque de prédation est inférieur ou égal à celui de l'habitat

plus sûr. Les deux habitats devraient ainsi être colonisés. Des phénomènes d'adaptation locale peuvent ensuite mener à une différentiation génotypique et phénotypique entre ces deux sous-populations et favoriser la variation sur des traits de personnalité comme la témérité ou l'exploration.

Malgré la pertinence et la simplicité théorique de ce modèle, peu d'études ont été capables de prouver que la variation sur les traits de personnalité trouve son origine dans un processus de sélection fréquence-dépendante. Certaines ont ainsi montré que des traits de personnalité étaient corrélés à l'utilisation d'une stratégie au sein d'un jeu fréquence-dépendant (Kurvers *et al.* 2010a). Par exemple, lorsqu'ils s'approvisionnent en groupe, les animaux peuvent utiliser différentes stratégies de recherche de nourriture : surveiller les découvertes des congénères afin de les rejoindre lorsqu'ils trouvent une parcelle de nourriture et la leur chaparder (stratégie « chapardeur »), ou chercher eux-mêmes leur source d'approvisionnement (stratégie « producteur »). L'utilisation de ces deux stratégies se révèle être fréquence-dépendante car le bénéfice lié au chapardage dépend de la quantité de nourriture d'une parcelle allant à son découvreur et de la proportion d'individus cherchant eux-mêmes la nourriture et chapardant (Barnard 1984 ; Giraldeau & Caraco 2000). Les bernaches nonettes téméraires sont ainsi moins susceptibles d'utiliser la stratégie « chapardeur » (Kurvers *et al.* 2010a). Chez cette espèce, la témérité est donc corrélée à des stratégies d'approvisionnement utilisées au sein d'un jeu fréquence-dépendant, ce qui suppose que la variation sur ce trait de personnalité puisse y être maintenue *via* l'utilisation différentielle de ces stratégies. Chez une espèce de lézard (*Eulamprus heatwolei*), les mâles utilisent deux tactiques alternatives de reproduction pour accéder aux femelles. Quarante pour-cent sont territoriaux, alors que le reste de mâles, appelés « *floaters* », naviguent à travers l'environnement. Stapley & Keogh (2004) ont montré que ces deux catégories de mâles différaient dans leur personnalité. Ainsi, les mâles « *floaters* » sont plus explorateurs que les territoriaux, mais montrent un temps de latence supérieur pour retourner s'approvisionner après avoir été victime d'une simulation d'attaque par un prédateur factice. La fréquence-dépendance de

l'utilisation de ces tactiques alternatives de reproduction n'a toutefois pas été mise en évidence chez cette espèce, contrairement à d'autres (Sinervo & Lively 1996). Cette étude suggère que la personnalité peut co-évoluer avec des tactiques alternatives de reproduction certainement soumises à une sélection fréquence-dépendante, même si d'autres études seraient nécessaires afin d'étayer cette hypothèse.

1.2.3.3. Le rôle des pressions de sélection fluctuantes

Les pressions de sélection fluctuantes représentent un mécanisme d'explication du maintien de la variation sur des traits phénotypiques, à travers la succession d'épisodes de sélection d'intensité et/ou de direction différentes. Ces pressions de sélection fluctuantes résultent de l'hétérogénéité environnementale spatiale et temporelle. Si le rôle des pressions de sélection fluctuantes a été régulièrement invoqué pour tenir compte du maintien de la variation sur la personnalité (Dingemanse *et al.* 2004), le rôle proximal précis de l'hétérogénéité environnementale n'a pas toujours été clairement identifié. Par exemple, une étude conduite sur une population de mésanges charbonnières a révélé des patrons de sélection fluctuants au cours des trois années de relevés sur le comportement d'exploration (figure 1.5. ; Dingemanse *et al.* 2004). Les auteurs suggérèrent que les pressions de sélection opposées entre les années et les sexes proviendraient de régimes de compétition fluctuants dus aux conditions climatiques variables entre les années. Ainsi, les femelles exploratrices rencontreraient un meilleur succès à la sortie d'hivers rudes lorsque la compétition pour la nourriture est intense. A l'inverse, les mâles explorateurs auraient un meilleur succès lors des hivers plus cléments grâce à un accès préférentiel aux territoires de reproduction au printemps. Ces interprétations *a posteriori* restent toutefois basées sur des résultats corrélationnels et des manipulations expérimentales seraient nécessaires afin d'isoler le rôle de différents types de compétition sur le succès des différentes personnalités. Les mêmes types de

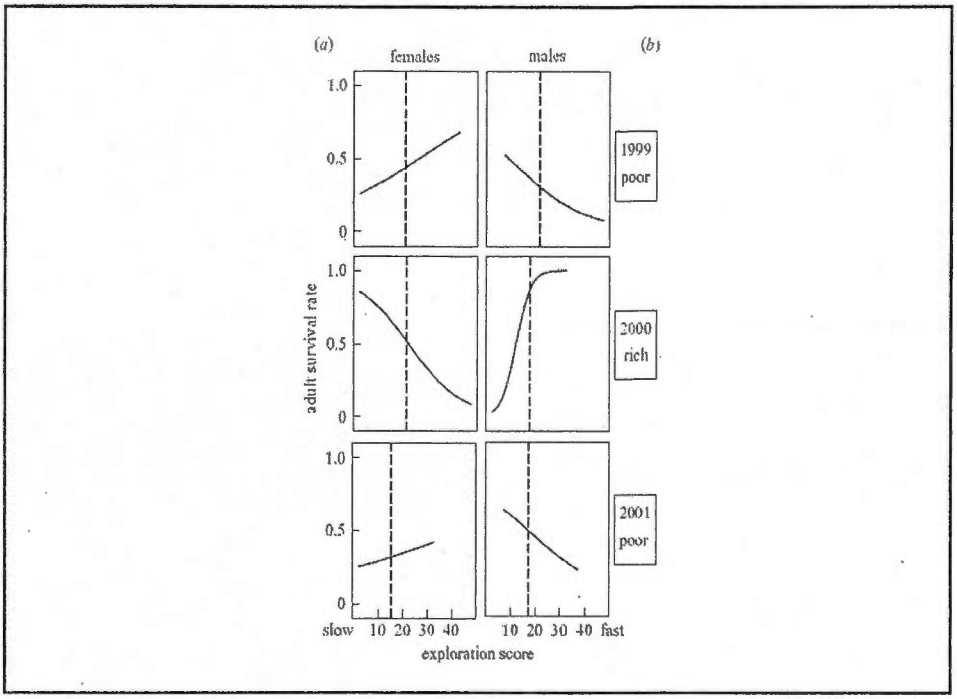

Figure 1.5. Graphiques illustrant les relations fluctuantes entre personnalité et aptitude phénotypique en fonction des années d'étude et du sexe chez la mésange charbonnière (issu de Dingemanse *et al.* 2004).

résultats ont été obtenus chez l'écureuil roux chez qui la relation entre l'agressivité de la mère et la survie de la progéniture fluctue au cours des années (Boon *et al.* 2007). Encore une fois, les auteurs suggèrent que l'abondance variable de la nourriture en fonction des années pourrait être responsable des effets différentiels de la personnalité sur l'aptitude de la progéniture.

En plus de ces travaux, d'autres études liant les variations de personnalité à certains facteurs écologiques soutiennent l'hypothèse que les variations environnementales pourraient être à l'origine des pressions de sélection fluctuantes contribuant au maintien de la variation sur la personnalité. Par exemple, Höjesjö *et al.* (2004) ont montré chez la truite commune (*Salmo trutta*) que le succès relatif des individus dominants par rapport aux subordonnés, quantifié par leur taux de

croissance et leur survie, dépendait de la complexité de leur environnement expérimental. Ainsi, au sein d'un environnement « simple », les individus subordonnés souffraient d'un taux de croissance et d'une survie plus faibles. Or, l'expérience en milieu plus « complexe » révéle un pattern opposé. Les auteurs suggèrent que la monopolisation des ressources par les poissons dominants, plus agressifs, est plus ou moins aisée en fonction de la complexité de l'habitat. Ces données expérimentales illustrent le caractère relatif et la dépendance à l'hétérogénéité environnementale spatiale de la relation entre personnalité, dominance et aptitude phénotypique. Enfin, la prédation a été proposée comme un facteur écologique primordial dans l'évolution de la personnalité. Álvarez & Bell (2007) ont établi que les individus provenant d'habitats différents variaient dans leur témérité chez l'épinoche à trois épines. Les poissons provenant d'étangs se montraient ainsi moins téméraires que les poissons de ruisseaux. Les auteurs ont suggéré que les deux habitats étudiés diffèrent dans le régime de prédation auquel ils sont soumis. Les individus originaires d'un habitat où le risque de prédation est plus élevé devraient ainsi se montrer moins téméraires que ceux provenant d'un habitat plus sûr.

Si le rôle des pressions de sélection fluctuantes dans l'évolution de la personnalité n'a pas encore été mis en évidence chez un large éventail d'espèces, certaines études suggèrent donc fortement que l'hétérogénéité environnementale spatiale et temporelle puisse engendrer des pressions de sélection variables à l'origine du maintien de la variation de la personnalité à diverses échelles du temps et de l'espace. Ainsi, les alternances saisonnière et annuelle, la complexité de l'habitat et ses caractéristiques intrinsèques biotiques et abiotiques sont autant de facteurs écologiques à l'origine de la diversité des écosystèmes et des environnements. Elles engendrent des pressions de sélection diverses, qui peuvent potentiellement modeler les distributions intra- et inter-populationnelle des traits de personnalité.

Les pressions de sélection fluctuantes représentent un mécanisme favorisant le maintien de la variation phénotypique au sein des populations. Ce mécanisme est donc adéquat pour expliquer l'une des caractéristiques du concept de personnalité : le

maintien de la variation intra-populationnelle. Toutefois, les pressions de sélection fluctuantes n'offrent aucune explication adaptative au regard de la constance intra-individuelle des traits de personnalité (mais voir Wilson *et al.* 1994). La dernière hypothèse évolutive qui sera explicitée ici possède justement l'avantage d'expliquer à la fois la constance intra-individuelle et la variation intra-populationnelle.

1.2.3.4. Le rôle des compromis évolutifs

L'apport du concept de compromis évolutif à l'étude de la personnalité réside dans la proposition que les traits de personnalité représentent les corrélats comportementaux de l'adoption de différentes trajectoires biodémographiques (Stamps 2007). Ainsi, les différences de productivité observées entre les organismes d'une même population et se situant sur le *continuum* du compromis croissance/mortalité auraient coévolué avec des différences de personnalité qui leur sont complémentaires. Par exemple, les organismes adoptant une croissance rapide, se reproduisant tôt, mais encourant un risque de mortalité plus élevé, notamment par une plus forte exposition à la prédation, seraient plus susceptibles de présenter des traits de personnalité favorisant l'adoption de cette trajectoire biodémographique. Ces mêmes organismes auraient ainsi toutes les chances d'être téméraires et agressifs, car une telle personnalité leur permettrait de profiter les premiers des opportunités d'approvisionnement et d'assurer des besoins énergétiques plus élevés (Careau *et al.* 2008), ou explorateurs, afin de maximiser la probabilité de découverte de nourriture. Ainsi, un modèle mathématique a établi que des différences dans le compromis entre la reproduction présente et future pouvaient effectivement conduire à la genèse et au maintien de la variation intra-populationnelle sur les traits de personnalité (Wolf *et al.* 2007). Au niveau empirique, certaines conditions sont nécessaires afin de pouvoir lier l'évolution de la personnalité aux compromis évolutifs et expliquer la constance intra-individuelle et la variation intra-populationnelle (Biro & Stamps 2008). Ainsi, les différences inter-individuelles de

productivité, soit la génération de biomasse *via* la croissance ou la reproduction, doivent être constantes pour favoriser la constance intra-individuelle des traits de personnalité. De plus, les traits de personnalité doivent être liés à la productivité des organismes pour pouvoir rendre compte de leur coévolution. En prenant appui sur des études conduites chez une vaste gamme d'espèces, Biro & Stamps (2008) ont ainsi démontré que les organismes provenant d'une même population différaient de manière constante dans leur productivité, et que cette constance pourrait être favorisée par les coûts à dévier de la trajectoire biodémographique, comme par exemple les coûts associés au phénomène de croissance compensatoire (Fisher *et al.* 2006). Ensuite, les traits de personnalité comme l'activité, la témérité, l'exploration ont été reliés à des composantes des stratégies biodémographiques telles que l'ingestion de nourriture, la croissance, la fécondité ou la survie chez de nombreuses espèces (Biro & Stamps 2008 ; Carter *et al.* 2010).). Dernièrement, Réale *et al.* (2010) ont tenté de transposer le concept du « syndrome du rythme de vie » (*pace of life syndrome*), bien documenté au niveau inter-spécifique, au niveau intra-populationnel. L'hypothèse du syndrome du rythme de vie suggère que des espèces proches devraient différer au niveau d'un ensemble de traits physiologiques ayant coévolués avec les stratégies biodémographiques propres à chaque espèce (Ricklefs & Wikelski 2002). Par exemple, les espèces d'oiseaux tropicaux vivent en général assez longtemps, produisent peu de jeunes par ponte, se développent lentement, sont matures tard dans leur vie et ont un taux métabolique faible (Wikelski *et al.* 2003 ; Wiersma *et al.* 2007). Ainsi, les oiseaux tropicaux présentent un rythme de vie plus lent au niveau de leur physiologie et de leurs stratégies biodémographiques que leurs homologues vivant en zones tempérées. L'intérêt du travail de Réale *et al.* (2010) a été d'inclure la dimension comportementale, dont les variations de personnalité au concept de syndrome du rythme de vie (Figure 1.6.), et de transposer cette approche aux variations inter-individuelles au niveau des populations d'une même espèce.

En conclusion, même si les hypothèses liées aux compromis de stratégies biodémographiques méritent d'être étayées et testées *via* d'autres études empiriques,

une large gamme de travaux suggère que les différentes facettes de la personnalité animale aient pu coévoluer avec les différentes trajectoires biodémographiques engendrées par les compromis évolutifs tels que le compromis croissance/mortalité ou le compromis entre reproduction actuelle et future. L'hypothèse du lien entre productivité et personnalité (Biro & Stamps 2008) présente l'avantage d'offrir un cadre théorique d'étude et des hypothèses pouvant être formulées *a priori* dans l'analyse de l'évolution de la personnalité et de ses relations avec le phénotype global.

Cette première partie aura donc permis de définir le concept de personnalité, d'évoquer ses origines et de comprendre pourquoi et comment les différences inter-individuelles sont devenues en ce début de siècle l'un des thèmes phares de l'écologie comportementale. Après une première phase quelque peu descriptive, l'étude de la personnalité animale s'est ensuite attachée à comprendre si celle-ci était soumise à la sélection naturelle et quels pouvaient être les facteurs écologiques puis évolutifs à l'origine de la constance intra-individuelle, de la variation intra-populationnelle et des corrélations entre traits (*i.e.* les syndromes comportementaux). Enfin, l'intérêt de l'étude de la personnalité réside dans sa relation avec de nombreux traits phénotypiques qui permet d'expliquer, au moins de façon mécanistique, de la variation jusque-là inexpliquée sur lesdits traits.

Les stratégies d'appariement et d'approvisionnement représentent deux composantes fondamentales de la vie des organismes. Etonnamment, le concept de personnalité a peu été étudié en contexte sexuel (Dingemanse & Réale 2005, voir Schuett *et al.* 2010 pour une synthèse) ou alimentaire. Les comportements de choix du partenaire par exemple révèlent pourtant une variation conséquente qui n'est pas prédite par les modèles classiques (Jennions & Petrie 1997), et qui pourrait trouver son origine dans des liens avec d'autres différences inter-individuelles. De plus, peu de crédit a été donné à l'hypothèse de l'évolution de la personnalité par sélection sexuelle, alors que les patterns d'appariement pourraient de manière logique contribuer à l'entretien du maintien de la variation sur des traits de personnalité

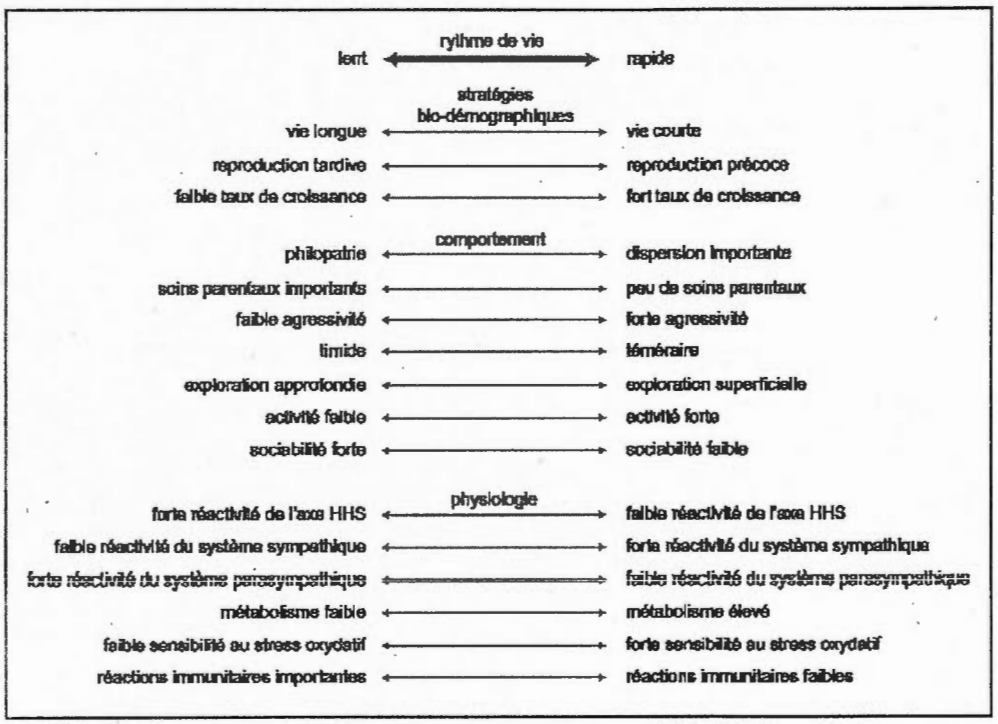

Figure 1.6. Schéma illustrant la possible intégration de différents traits le long du continuum du rythme de vie (adapté de Réale *et al.* 2010).

(Groothuis & Carere 2005 ; Sinn *et al.* 2006). Nous nous attacherons ainsi dans la prochaine partie à analyser les quelques études traitant des liens entre personnalité et stratégies d'appariement, puis mettront en avant les points qui n'ont pas été explorés et mériteraient des approfondissements. Dans une seconde partie, nous aborderons les liens entre personnalité et stratégies d'approvisionnement en groupe. Comme il a été envisagé par l'hypothèse de Biro & Stamps (2008), les activités d'approvisionnement pourraient être un facteur primordial dans l'évolution des différents traits de personnalité au sein du contexte des compromis évolutifs. Plus précisément, les liens entre personnalité et approvisionnement social au travers de différents types de compétition ne font l'objet que d'investigations éparses dans la littérature (Kurvers *et al.* 2010a). Nous décrirons ainsi les quelques études en ayant fait l'objet, puis

fournirons des pistes d'investigation des liens entre personnalité et stratégies d'approvisionnement.

1.3. PERSONNALITÉ ET STRATÉGIES D'APPROVISIONNEMENT EN GROUPE

Comme pour la sélection sexuelle, les relations entre personnalité et stratégies d'approvisionnement en groupe peuvent être abordées sous deux angles d'études : l'explication de la variation dans les stratégies d'approvisionnement par les variations de personnalité ; et l'évolution de la personnalité à travers le succès des différentes stratégies d'approvisionnement. Encore une fois, la covariance entre l'intensité d'un trait de personnalité donné et le mode d'approvisionnement occupe une place centrale dans l'étude du lien entre ces deux variables sous ces deux différents angles. De plus, comme expliqué dans l'introduction générale, les comportements d'approvisionnement sont au cœur de certaines hypothèses évolutives proposées pour rendre compte de l'évolution des personnalités. Ainsi, sous l'hypothèse des pressions de sélection fluctuantes, il a été suggéré que l'hétérogénéité environnementale temporelle et spatiale module l'intensité de la compétition alimentaire, ce qui aurait pour effet d'engendrer des pressions de sélection variables au cours des années potentiellement responsables du maintien de la variation sur les traits de personnalité (Dingemanse *et al.* 2004 ; Boon *et al.* 2007). De plus, sous l'hypothèse de la coévolution entre compromis évolutifs et personnalité (Biro & Stamps 2008), l'accès aux ressources alimentaires, leur monopolisation, et le taux d'ingestion, sont les facteurs liant les traits de personnalité aux différences de productivité et de position au sein des compromis évolutifs. La personnalité y est considérée comme le volet comportemental, ayant évoluée de manière adaptative pour correspondre de manière fonctionnelle au volume d'énergie requis par un type d'individu donné (Biro & Stamps 2008 ; Careau *et al.* 2008).

Les stratégies d'approvisionnement en groupe sont classiquement étudiées à travers deux types de compétition : la compétition par interférence, désignant l'acquisition de ressources à la suite d'interactions physiques entre les compétiteurs, et la compétition par exploitation, basée sur la détection et l'efficacité d'exploitation des ressources sans interaction directe avec les congénères. Ces deux types de compétition mettent généralement en exergue des capacités et des traits phénotypiques différents de la part des individus impliqués. Le succès au sein de la compétition par interférence sera plutôt prédit par la taille, l'agressivité des individus, et plus généralement, par leur capacité à monopoliser l'accès aux ressources. A l'inverse, la compétition par exploitation devrait mettre en avant la capacité des organismes à détecter les ressources, à utiliser de manière optimale les informations personnelles et sociales quant à leur localisation et leur profitabilité. Les deux types de compétition sont donc généralement étudiés de manière distincte, et il en va de même pour l'analyse de leurs liens avec la personnalité des compétiteurs. Par exemple, chez les mésanges charbonnières, les mâles territoriaux explorateurs dominent les mâles peu explorateurs dans l'accès à une source d'approvisionnement unique (Dingemanse & de Goede 2004). A l'inverse, chez les juvéniles, ce sont les individus peu explorateurs qui sont dominants par rapport aux explorateurs. La relation entre personnalité et dominance semble donc dépendre du contexte chez cette espèce. Chez la mésange de Gambel, les individus peu explorateurs dominent les individus explorateurs (Fox *et al.* 2009). A l'inverse, chez l'épinoche à trois épines ou la perche commune (*Perca fluviatilis*), les individus téméraires ont un accès préférentiel à la nourriture face aux individus timides (Ward *et al.* 2004 ; Westerberg *et al.* 2004). La personnalité peut donc influencer de manière différentielle la probabilité de devenir dominant lors d'un épisode de compétition par interférence en fonction des espèces. Le lien entre personnalité et accès à la nourriture en situation de compétition par interférence semble donc difficile à prédire sur la seule base de la personnalité des individus. Certaines études mettent en avant un lien complexe entre personnalité, compétition par exploitation et compétition par interférence. Ainsi, chez

le mouton (*Ovis aries*), les individus téméraires sont plus susceptibles de s'éloigner du groupe s'approvisionnant et d'initier la formation de sous-groupes (Michelena *et al.* 2009). Ce comportement permet de réduire la densité d'individus exploitant la même parcelle alimentaire. Chez le guppy, Dyer *et al.* (2009) ont montré que les groupes mixtes, expérimentalement constitués de deux individus téméraires et de deux individus timides, ont une composition permettant à plus d'individus de s'approvisionner que les groupes composés de quatre individus téméraires ou timides. Cette étude suggère que les organismes peuvent avoir intérêt à s'associer à des congénères de personnalité opposée lors de l'approvisionnement en groupe. Les bénéfices de compositions mixtes pourraient être liés à une meilleure coordination dans l'approche de la nourriture et possiblement à une réduction de la compétition par interférence (Dyer *et al.* 2009). De plus, les auteurs suggèrent que ces bénéfices pourraient contribuer au maintien de variations de témérité dans les populations de guppies.

Ces études soulignent donc le rôle de la personnalité dans l'adoption des différentes stratégies d'approvisionnement et ses conséquences sur l'issue de chaque type de compétition. Dans le même temps, la variation sur les traits de personnalité semble pouvoir être favorisée par la diversité des conséquences de l'approvisionnement en groupe et des stratégies adoptées. L'influence de la personnalité sur la compétition par exploitation n'a pourtant fait l'objet que d'une seule étude jusqu'à présent (Kurvers *et al.* 2010a). Au sein du jeu producteur-chapardeur (Barnard & Sibly 1981 ; Giraldeau & Caraco 2000), les bernaches nonettes qualifiées de timides utilisent plus fréquemment la tactique de chapardage que les individus téméraires (Kurvers *et al.* 2010a). La personnalité influencerait donc l'utilisation différentielle des informations personnelles et sociale (Marchetti & Drent 2000 ; Nomakuchi *et al.* 2009 ; Kurvers *et al.* 2010b) qui mènerait à des comportements d'approvisionnements alternatifs. Toutefois, l'importance et l'étendue de ces résultats restent méconnues et méritent des investigations chez d'autres espèces. L'étude du lien entre stratégies d'approvisionnement et personnalité est un

domaine prometteur pour la compréhension du maintien de la variabilité sur les traits de personnalité par : 1) l'adoption différentielle de tactiques alternatives d'approvisionnement reliée à la personnalité (Kurvers *et al.* 2010a), et 2) les conséquences de la composition des groupes sur le succès *per capita* (Dyer *et al.* 2009). De plus, l'analyse de la personnalité des organismes engagés dans une compétition pour les ressources alimentaires permet d'en identifier et d'en prédire les conséquences en termes d'aptitude phénotypique individuelle. De manière intéressante, la personnalité pourrait être considérée comme une contrainte phénotypique influençant la probabilité des individus d'adopter telle ou telle stratégie au sein d'un jeu fréquence-dépendant. Les organismes pourraient ne pas être entièrement flexibles et s'ajuster de manière adaptative aux conditions sociales par exemple. Cette contrainte pourrait conduire les groupes s'approvisionnant à ne pas atteindre la fréquence d'utilisation des tactiques à l'équilibre prédite par la théorie dans des jeux fréquence-dépendant comme le jeu producteur-chapardeur. La prise en compte de la personnalité des individus impliqués pourrait ainsi permettre d'expliquer la variabilité observée dans la tendance des groupes à montrer une utilisation des tactiques alternatives d'approvisionnement conforme aux fréquences attendues à l'équilibre. Enfin, l'étude de la personnalité en contexte d'approvisionnement amène à considérer les deux types de compétition comme deux situations différentes au sein desquelles la personnalité pourrait avoir des conséquences variables dans la mesure où les deux types de compétition ne mettent pas en avant les mêmes caractéristiques phénotypiques individuelles. L'évolution de la personnalité en contexte d'approvisionnement mérite ainsi d'être évaluée à la fois à travers la compétition par exploitation et la compétition par interférence.

Une partie de cette thèse sera donc consacrée à déterminer dans quelle mesure les variations inter-individuelles de personnalité permettent de prédire l'utilisation de tactiques alternatives d'approvisionnement au sein d'un jeu producteur-chapardeur, et d'en déterminer les conséquences en termes de succès d'approvisionnement en fonction des personnalités. En complément, l'étude de

l'influence des personnalités sur l'issue de la compétition par interférence favorisera la comparaison de leurs aptitudes à travers différentes situations au sein du même contexte.

1.4. PERSONNALITÉ ET STRATÉGIES D'APPARIEMENT

L'intérêt de l'étude des relations entre personnalité et stratégies d'appariement se situe à plusieurs niveaux. Le premier est de tenter d'expliquer les variations de préférence sexuelle et de choix du partenaire couramment observées au sein des populations animales, et qui n'ont jamais été prédites par les modèles d'évolution des caractères sexuels secondaires mâles (Jennions & Petrie 1997 ; Widemo & Saether 1999). Le deuxième est de déterminer si la sélection inter-sexuelle peut contribuer au maintien de la variation des traits de personnalité. Le succès d'appariement et le succès reproducteur représentant deux composantes majeures de l'aptitude phénotypique individuelle, la variation dont elles font preuve, ainsi que les facteurs les influençant (*e.g.* la personnalité) devraient être soumis à une forte sélection. A ce jour, seules deux études ont mis en évidence que la personnalité des mâles pouvait faire l'objet de la préférence des femelles (Godin & Dugatkin 1996 ; Schuett *et al.* sous presse). Ainsi, chez les guppies, l'intensité de la coloration orangée est corrélée à la témérité, évaluée lors du comportement d'inspection d'un prédateur. Godin & Dugatkin (1996) ont réussi à démontrer expérimentalement que les femelles expriment une préférence pour les mâles plus orangés lorsque le risque de prédation est nul, quel que soit le comportement du mâle. Toutefois, en présence d'un prédateur, les femelles préfèrent les mâles téméraires, quelle que soit l'intensité de leur coloration. Chez les guppies, le trait de personnalité « téméraire » fait ainsi l'objet d'une préférence des femelles et peut évoluer par sélection inter-sexuelle. Chez les Diamants mandarins, les femelles présentant des tendances exploratoires fortes et intermédiaires préfèrent les mâles rendus expérimentalement plus

explorateurs (Schuett *et al.* sous presse), alors que les femelles peu exploratrices n'expriment pas de préférence marquée. D'autres études ont mis en évidence une préférence des femelles pour un certain type de personnalité mâle, sans en isoler toutefois le rôle ; ce qui laisse la possibilité que l'objet de la préférence des femelles soit un autre trait phénotypique qui serait lui-même corrélé à la personnalité du mâle. Ainsi, les mésanges charbonnières mâles artificiellement sélectionnées pour des hauts niveaux d'exploration montrent une préférence pour les femelles très exploratrices, contrairement aux mâles peu explorateurs (Groothuis & Carere 2005). Enfin, Reaney & Backwell (2007) ont montré chez une espèce de crabe (*Uca mjoebergi*) que les mâles les plus téméraires ne reçoivent pas plus de visites de la part des femelles que les mâles timides, mais montrent une plus forte probabilité d'appariement.

Même si l'effet spécifique de la personnalité est difficile à isoler expérimentalement, certains travaux prouvent que des traits de personnalité peuvent être la cible de la préférence sexuelle des femelles. La sélection inter-sexuelle représente ainsi un processus évolutif contribuant à l'évolution de la personnalité.

L'objet et la direction du choix des femelles renseignent sur les associations potentiellement fructueuses en termes de succès reproducteur associé à un trait phénotypique donné. A partir des expériences précédentes, on peut par exemple s'attendre chez les Diamants mandarins à ce que les appariements entre individus très explorateurs mènent à un meilleur succès reproducteur individuel que si un explorateur s'associait à un autre oiseau peu explorateur. A l'inverse, aucune différence du point de vue des individus peu explorateurs n'est attendue en fonction de la personnalité de leur partenaire, étant donné que les premiers n'expriment aucune préférence claire. Ces données nous permettent, à partir des préférences sexuelles, d'inférer les pressions de sélection s'exerçant sur les individus en supposant qu'ils effectuent un choix optimal. Certaines études sont allées plus loin en quantifiant le succès reproducteur de différentes associations entre partenaires de personnalité connue. A l'inverse, ce type de données fournit des prédictions quant à la direction

des préférences sexuelles que les individus devraient exprimer. Plus globalement, ce genre d'études permet d'inférer la covariance entre l'intensité du trait de personnalité et l'aptitude phénotypique à partir de la détermination de l'aptitude de la progéniture, et donc des associations entre parents. Enfin, le type d'association, hétéro- ou homogame, en fonction de la personnalité des partenaires devraient prédire les pressions de sélection agissant sur le *continuum* de variation de ce trait. Ainsi, hormis toute relation potentielle de dominance génétique, les associations hétérogames devraient contribuer à réduire la variation sur le trait de personnalité par la production d'une progéniture présentant un phénotype intermédiaire (Hunt *et al.* 2007), alors que les associations homogames devraient engendrer une progéniture au phénotype identique à celui des parents, donc contribuer au maintien de la variation lorsque le phénotype des parents est situé à un extrême du *continuum* de personnalité (Kondrashov & Shpak 1998). Chez les Diamants mandarins, des expériences d'élevage et de reproduction avec adoption croisée (*cross-fostering* en anglais), ont montré que les partenaires d'intensités d'exploration similaires élevaient des jeunes en meilleure condition que les couples désassortis (Schuett *et al.* 2011). De la même manière, les couples homogames élevaient des jeunes en meilleure condition que les couples hétérogames dans une population naturelle de mésanges charbonnières (Both *et al.* 2005). Enfin, chez des seiches, les reproductions les plus fructueuses semblent se produire lorsque les partenaires sont assortis par niveaux de témérité (Sinn *et al.* 2006). Ainsi, pour ces trois dernières espèces, on peut s'attendre à des patterns de préférences des femelles, et même des mâles dans le cas des organismes monogames, relativement clairs. Les individus devraient choisir des partenaires sexuels dont la personnalité leur est similaire. Ces études nous permettent donc de formuler des prédictions quant aux comportements sexuels des organismes. Ensuite, elles fournissent un moyen d'estimer l'aptitude phénotypique liée à un *continuum* de valeurs du trait de personnalité, par l'évaluation des composantes de l'aptitude phénotypique telles que le taux de croissance ou la condition de la progéniture à maturité, et le succès reproducteur, pour les parents exclusivement.

Une autre catégorie d'expérimentation offerte par l'étude de la personnalité en contexte sexuel concerne l'explication de la variation observée dans les comportements sexuels. Le choix d'un partenaire se définit par une longue chaine de phénomènes cognitifs successifs (Bateson & Healy 2005) dont la tactique d'échantillonnage, l'expression de la préférence et le taux de réponse des femelles sont trois résultantes comportementales classiquement évaluées (Reinhold *et al.* 2002 ; Bailey 2008). Ces composantes du choix du partenaire sont autant de facteurs pouvant faire preuve d'un certain degré de variation dont les conséquences sur l'évolution des traits phénotypiques mâles restent méconnues (Brooks & Endler 2001 ; Bailey 2008). Ainsi, l'identification des facteurs responsables de la variation des comportements sexuels permettrait d'en comprendre les causes, d'en prédire les conséquences et d'expliquer son occurrence *via* la coévolution avec d'autres traits phénotypiques. De nombreuses études mettent en évidence une variation inter-individuelle constante des comportements de choix des femelles (Brooks & Endler 2001 ; Reinhold *et al.* 2002 ; Forstmeier & Birkhead 2004 ; Forstmeier 2007). Toutefois, l'influence potentielle de leur personnalité sur ses comportements n'a été que rarement étudiée (van Oers *et al.* 2008 ; While *et al.* 2009). Par exemple, chez les Diamants mandarins, la littérature abonde de travaux liant la coloration du bec des mâles ou leur chant à la préférence des femelles (Birkhead *et al.* 1998 ; Blount *et al.* 2003 ; Holveck & Riebel 2007). En dépit de la quantité d'études sur ce sujet, aucun consensus n'émerge actuellement et les résultats mettent tantôt en avant une préférence pour les becs intensément colorés ou pour un taux de chant soutenu, et tantôt manquent de cibler l'objet de la préférence des femelles (Collins & ten Cate 1996). Encore une fois, peu d'études ont jusqu'à maintenant étudié l'influence de la personnalité de cette espèce modèle sur les différentes composantes du choix des femelles, ni abordé les conséquences en termes d'estimation expérimentale des composantes du choix du partenaire, ou d'évolution des traits mâles (Schuett 2008).

Une partie de cette thèse sera donc consacrée à déterminer dans quelle mesure les variations de personnalité entre femelles permettent de rendre compte de la variation observée sur certaines composantes du choix du partenaire telles que la sélectivité, ou tactiques d'échantillonnage, et la préférence sexuelle. De plus, une revue critique des articles publiés, accompagnée de perspectives d'études et théoriques liant personnalité et sélection sexuelle achèvera de déterminer dans quelle mesure la personnalité peut influencer les processus de sélection intra- et inter-sexuelle et comment la sélection sexuelle peut contribuer à l'évolution des personnalités.

L'ensemble des manipulations de la présente thèse a été conduit sur des Diamants mandarins, une espèce de passereau exotique originaire d'Océanie (figure 1.7.). Ces oiseaux sont très largement utilisés en écologie comportementale pour des expériences en captivité portant à la fois sur le choix du partenaire (Witte 2006 ; Holveck & Riebel 2009), la personnalité (Schuett 2008 ; Schuett & Dall 2009), ou

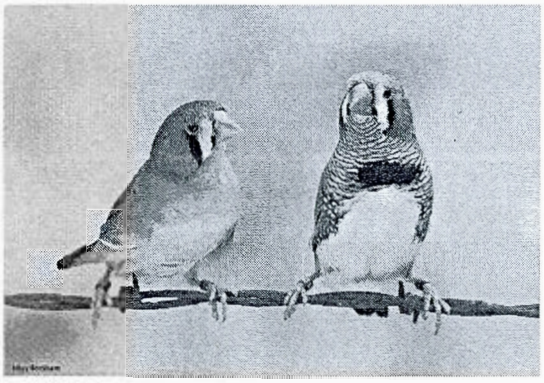

Figure 1.7. Photographie d'un couple de Diamants mandarins. La femelle est à gauche et le mâle à droite.

l'approvisionnement social (Beauchamp 2006). Cette espèce grégaire se reproduit de manière opportuniste à la faveur de pluies abondantes et forme des couples monogames perdurant sur plusieurs saisons de reproduction (Zann 1996).

Ce manuscrit de thèse sera ainsi organisé en trois grandes parties successives. La première partie abordera des questions d'ordre méthodologique avec l'étude des corrélations entre traits de personnalité au sein de la population de Diamants mandarins (i.e. syndrome comportemental), puis l'intérêt de différentes techniques de mesures pour l'évaluation de la personnalité. Enfin, l'importance des biais que peuvent engendrer les différences de personnalité dans les études de mesure du choix de partenaire dans les tests d'association spatiale classiquement utilisés sera présentée. La deuxième partie sera consacrée à l'étude des liens entre personnalité et comportements d'approvisionnement. Un premier article traitera des effets concomitants de la personnalité et de la condition corporelle des individus sur leur motivation à s'alimenter. Un deuxième sera consacré à l'influence de la personnalité sur les stratégies d'approvisionnement en groupe, soit l'adoption des tactiques producteur ou chapardeur par l'utilisation différentielle de l'information personnelle et sociale. Enfin, la troisième partie portera sur les liens entre sélection sexuelle et personnalité, avec une étude de l'influence de la personnalité sur l'utilisation de l'information sociale, cette fois en contexte d'appariement (i.e. l'imitation du choix du partenaire), puis un article de synthèse portant sur l'importance et l'intérêt de l'étude simultanée de la personnalité animale et des processus de sélection sexuelle.

ARTICLE I

PERSONALITY PREDICTS SOCIAL DOMINANCE IN FEMALE ZEBRA FINCHES *TAENIOPYGIA GUTTATA*, IN A FEEDING CONTEXT

Morgan David, Yannick Auclair & Frank Cézilly

Animal Behaviour 81, 219-224

2.1. ABSTRACT

Although personality has been defined as a *suite* of correlated behaviours, most studies of animal personality actually consider correlations between a few traits. Here we examined the repeatability and correlational structure of five potential personality traits (activity, neophobia, exploratory tendencies, risk taking behaviour, and obstinacy), in female zebra finches, *Taeniopygia guttata*. In addition, we assessed to what extent personality influenced social dominance in a feeding context in this gregarious species. All personality traits were found to be highly repeatable within individuals. In addition, except for obstinacy, all of them were found related to each other, thus defining a behavioural syndrome. Social dominance was predicted by personality, with proactive individuals being more likely to be dominant. Our results suggest that personality can be considered as a new static factor influencing within-group hierarchies. We finally discuss these results in terms of the consequences on the evolution of personalities and the need to take several traits into account to provide full descriptions of individual personality.

Keywords: behavioural syndrome, competition, dominance, false discovery rate, feeding success, hierarchy, life-history productivity, personality, repeatability, zebra finch

2.2. INTRODUCTION

Consistent individual differences in behaviour across various contexts and situations are of increasing interest to behavioural ecologists (Sih et al. 2004a; Réale et al. 2007). Several studies have shown that individual variation in personality can have fitness consequences, (see Smith & Blumstein 2008 for a review). For instance, survival between two breeding seasons was found to be related to personality in female red squirrels, *Tamiasciurus hudsonicus* (Boon et al. 2008), whereas the influence of personality on survival varies according to population density in the common lizard, *Lacerta vivipara* (Cote et al. 2008). Reproductive fitness can also be influenced by personality, as shown by recent evidence in fish (Wilson et al. 2010a), birds (Van Oers et al. 2008) and mammals (Réale et al. 2009). In addition, individual variation in personality can be repeatable (Quinn et al. 2009; Wilson & Godin 2009) and linked to genetic variation (van Oers et al. 2004a,b; Fidler et al. 2007), suggesting that variation in personality can be exposed to natural selection.

Assessing the ecological relevance of personality, both between and within species (Uher 2008), requires, however, that personality is assessed in some standardized way. Although personality has been defined as a *suite* of correlated behaviours expressed either within a given behavioural context or across different contexts (Sih et al. 2004b), most studies of animal personality consider in practice correlations between a few traits, focusing eventually on only two aspects of personality such as, for instance, exploration and risk taking (Brodin 2009; Harcourt et al. 2009; but see Wilson et al. 2010b). This is in strong contrast to studies of personality in human beings, where personality is assessed from patterns of covariation of traits belonging to several broad factors (McCrae et al. 1998; Uher 2008). Recent studies of human personality suggest, however, that measuring only a few personality traits might be insufficient to predict complex behaviours (Paunonen et al. 2003; Ashton & Lee 2007; de Vries et al. 2009). In particular, using a larger number of factors is recommended to reduce error in behaviour prediction and

increase accuracy in behaviour explanation (Paunonen & Ashton 2001), particularly in the case of relatively complex behaviours, which can be considered multidimensional and multidetermined (Paunonen et al. 2003).

Although various constraints can limit the number of personality dimensions that can be quantified using free-ranging individuals, experiments with captive individuals may allow a deeper consideration of the multidimensional nature of personality. The present study was precisely designed to investigate consistent differences in personality between individuals, while considering simultaneously several dimensions of personality. To that end, we quantified a series of traits previously used to estimate personality in birds in a non-social context, and assessed the correlational structure between those traits. We then investigated to what extent variation in personality was a predictor of dominance status (Fox et al. 2009), a character known to have a strong influence on fitness in socially living organisms (Ellis 1995; Koivula et al. 1996; Mennill et al. 2004), and to be potentially influenced by personality in the wild (Dingemanse et al. 2004; Fox et al. 2009). Following the "life-history productivity" hypothesis (Biro & Stamps 2008), according to which some individuals express a personality enabling them to sustain a high productivity, we predict that such proactive individuals should have a preferential access to food through dominance. The Zebra finch, *Taeniopygia guttata*, was chosen as our model organism as it is a highly social bird species that is regularly used in experimental studies of behaviour (Zann 1996), including personality (Martins et al. 2007; Schuett & Dall 2009).

2.3. METHODS

2.3.1. Biological Model

Forty-two wild-type and virgin, but sexually mature, female zebra finches were purchased from a reliable local supplier and used in this study. Only females were

used, as the present study was part of a larger research program on the influence of personality on female sexual behaviour. Birds were kept in a single experimental room and maintained in individual cages (60×33×30 cm), containing four perches at different heights, four feeders with food and water. Room temperature was maintained at 22 ± 2°C and the photoperiod was 13:11h light:dark cycle (0730 am-0830 pm), with a 30-minute period simulating dawn and dusk through increasing and decreasing light intensity in the morning and evening. Each individual was identified by an orange numbered ring (AC Hugues, UK, size XF). Birds were provisioned with millet seeds, cuttlebones and water ad libitum. Vegetables were only given outside of the experiment periods. Birds were not given any additional vitamins. One bird looking ill and showing little activity had to be discarded during the experiments, reducing our sample size to 41 individuals. The bird seemed not able to cope with a new stressful situation. It was then isolated and provided with vitamins before recovering. However, it was then not re-included within the experiment. At the end of the experiment, birds were kept in groups of two to be used in subsequent studies. The experimental procedures were in agreement with the ethical requirements of the Université de Bourgogne.

2.3.2. Personality Traits

Each trait was assessed twice for each individual at a one-week interval.

2.3.3. Exploratory tendencies

Following previous studies of exploratory behaviour in birds (Dingemanse et al. 2002; Drent et al. 2003; van Oers et al. 2004a), individual exploratory tendencies were assessed in a large, unfamiliar cage (140×140×70 cm) with opaque walls and a Plexiglas ceiling, inside which five artificial trees, composed of four small branches

each, were set. Birds were food-deprived for one hour before being introduced in a black box placed against a small sliding door on one side of the apparatus. Experimenters then gently opened the door with a pulley system from outside the room. From that moment, individual behaviour inside the apparatus was recorded for one hour, using a video-camera (JVC Everio GZ-MG20) placed one metre above the cage. During the analysis, experimenters recorded the number of movements between trees and between branches of a single tree. The cumulative number of movements was subsequently taken as a measure of exploration tendencies.

2.3.4. Neophobia

Neophobia was assessed using the novel object test procedure (Boogert et al. 2006; Tobler & Sandell 2007; Spencer & Verhulst 2007). After one hour of food deprivation, an unfamiliar object was introduced within the cage at 10 cm from the unique feeder. We used a different object (a small bag or a soccer figurine) on the first and second trial to avoid habituation, with the order of presentation being randomly chosen for each bird. Individual behaviour was then video-recorded for 15 minutes. Experimenters recorded latency to perch within 15 cm of the feeder, latency to reach the feeder and take seeds, the number of times the birds came feeding, the number of times they perched near the feeder, and the amount of time spent feeding (in seconds). Mean values were calculated from both trials for each measure and a Principal Component Analysis (PCA) was performed on all measures to synthesize them into a single value of neophobia (first axis explained 71.92 % of variance; eigenvectors: latency to perch near the feeder: -0.42; number of times on the perch: 0.46, latency to reach the feeder: -0.46; number of feeding events: 0.48; time spent feeding: 0.41). Neophobia score was then negatively related to the actual degree of neophobia, with low values characterizing neophobic individuals. For convenience, we reversed neophobia scores for subsequent analysis, such that higher values

correspond to neophobic individuals. Due to an accident, the behavioural measures recorded in the "small bag" conditions were missing for one individual, reducing our sample size to 40 individuals when testing the influence of the type of object on neophobia. For this particular individual, we then only considered the behavioural measures in front of the soccer figurine for the neophobia test.

2.3.5. Activity

Intrinsic activity was video-recorded in individual home cages immediately before neophobia test. Birds were food-deprived for one hour before each trial, and had no access to any food source during it. Following the time-sampling technique (Martin & Bateson 1993), experimenters assigned a score of one if the birds had moved between two perches or of an equivalent distance on the floor during the last five seconds. As activity was assessed during ten minutes, individuals could then receive a maximal score of 120. When staying still, birds were assigned a score of zero.

2.3.6. Startle test

Startle tests classically assess latency to resume foraging after a stressful event (Martins et al. 2007). Birds were food-deprived for one hour before the trial, after which the feeder was reintroduced in the cage with two washers wedged between the feeder top and the trap door above it, connected with a thin thread to the outside of the room. Experimenters then gently pulled the thread when the individual started feeding, creating vibrations on the feeder and a brief sound, which successfully frightened the bird off the feeder. Latency to resume foraging after that startle was then recorded live with a stopwatch and a miniature video-camera placed one metre in front of the cage and linked to a monitor outside of the room. Individuals were given a latency time of 601 seconds if they failed to resume foraging at the feeder

during the ten minutes. For convenience, "reaction to startle" scores were reversed for subsequent analyses, such that birds taking longer to resume foraging obtained lower scores.

2.3.7. Struggle rate or obstinacy

The intensity of individual struggling after catching is commonly assessed in studies of personality in mammals (Réale et al. 2000; Boon et al. 2007; Martin & Réale 2008), although, to our knowledge, such a test has never been used with birds. Individuals were caught and put on a flat surface below a small landing net (20×15 cm). Time needed to catch the bird in the home cage and numbers of hops and escape attempts under the net were recorded during 30 seconds. All manipulations were done by M.D. Struggle rate was considered as a measure of individual obstinacy.

2.3.8. Aggressiveness and Social Dominance

Aggressiveness and social dominance were both assessed in groups of six individuals wearing different colour rings (light grey, light yellow, orange, black, blue and purple; Animalerie Nation, France) to allow individual identification. Individuals were randomly allocated to the seven different groups. Groups were maintained in large cages (100×50×50 cm) for ten days before the tests, allowing individuals to interact freely in the meanwhile. Birds were starved for one hour before trials to enhance motivation to feed. Social dominance was assessed through the access order to a single feeder (Boogert et al. 2006; Val-Laillet et al. 2008), the monopolization of resources and aggressiveness, as previously done in other species (Duckworth et al. 2004; Boogert et al. 2006). Within-group interactions were then recorded twice on two consecutive days in a feeding context. Individuals were food-deprived for one hour before the start of each experiment. Experimenters then placed a unique feeder

allowing only one bird to feed at a time at the extreme side of the cage. Trials were video-recorded for 15 minutes with a miniature camera (Typhoon Easycam) following the introduction of the feeder. Interactions at the feeder mainly consisted of chases and displacements. Pecking was rare, and no bird was injured in the course of the trials. During the analysis, the experimenters measured the access order to the feeder, such that the first bird to reach the feeder was given a score of 1, the second was given a score of 2, and so on until score 6. The number of agonistic interactions (displacement from the feeder and in its surrounding) and identities of birds involved, the number of times at the feeder and the total time spent feeding were also recorded. Thus, access order to the feeder, number of given aggressive acts, time spent at the feeder, and number of times at the feeder were all separately used to assess social dominance. We assumed that the birds reaching the feeder first, spending more time at the feeder and showing a high level of aggressiveness were the dominant birds (Boogert et al. 2006).

2.3.9. Morphometric Measures

All morphometric measures were taken twice on two different days by Y.A. Values were then averaged for each bird. Tarsus length was measured with a digital calliper to the nearest 0.1 mm. Birds were weighted to the nearest 0.01 g with an electronic balance (OHAUS, Scout Pro SPU202). We determined a Body Condition Index (BCI) corresponding to residuals calculated from the linear regression of log (weight) on log (tarsus length). Measures were significantly repeatable: tarsus length: $r = 0.73$, $P < 0.0001$; weight: $r = 0.98$, $P < 0.0001$.

2.3.10. Data Analysis

Consistency in personality was assessed through calculating behaviour repeatability between the two trials, using Lessels & Boag (1987)'s method. For each personality traits, mean values were calculated from both trials and use thereafter. The existence of a behavioural syndrome was then assessed from the correlations between personality traits. As multiple correlations were performed to test the relationships between personality traits, it was necessary to control for type I errors. Hence, as an alternative to Bonferroni correction (see Moran 2003; Nakagawa 2004), we relied on the procedure introduced by Benjamini & Hochberg (1995), which is similar to Bonferroni's, but also reduces type II errors through controlling for the false discovery rate (Verhoeven et al. 2005). All analyses were conducted using JMP 5.0.1 statistical software (SAS Institute, Cary, NC). Only two-tailed tests were used. Variables were log-, square root- or arcsine square-root-transformed to reach normality when needed.

2.4. RESULTS

2.4.1. Evidence for a Behavioural Syndrome

Personality traits were highly consistent between successive trials (neophobia: R = 0.43, $F_{40,80}$ = 2.51, P = 0.002; activity: R = 0.40, $F_{40,80}$ = 2.15, P = 0.004; exploration: R = 0.81, $F_{40,80}$ = 9.67, $P < 0.0001$; reaction to startle: R = 0.37, $F_{40,80}$ = 2.19, P = 0.009; obstinacy: R = 0.43, $F_{40,80}$ = 2.48, P = 0.002). During the neophobia tests, birds took longer to perch within 15 cm from the feeder (paired t test: t_{39} = -2.71, P = 0.010) and to reach the feeder (t_{39} = -2.82, P = 0.001) when facing the small bag than when facing the soccer figurine. Relationships between personality traits enabled us to define a "behavioural syndrome" within our study group (tableau 2.1., figure 2.1.). Only obstinacy was not related to any other trait. A PCA was thus

performed on all traits, except obstinacy, to reduce individual personality to a single value thereafter called the personality synthetic value. The first axis explained 51.26 % of variance. Eigenvectors of each personality traits on the axis are given as follow: exploration: 0.46; activity: 0.53; neophobia: 0.52; reaction to startle: -0.50. The frequency distribution of the personality synthetic values is shown in figure 2.2. Individuals defined by a high value were more exploratory, active, bolder and quicker to resume feeding after the startle. Within the continuum of personality synthetic values, they were therefore categorized as "proactive", whereas individuals possessing lower values were categorized as "reactive" (Réale et al. 2007).

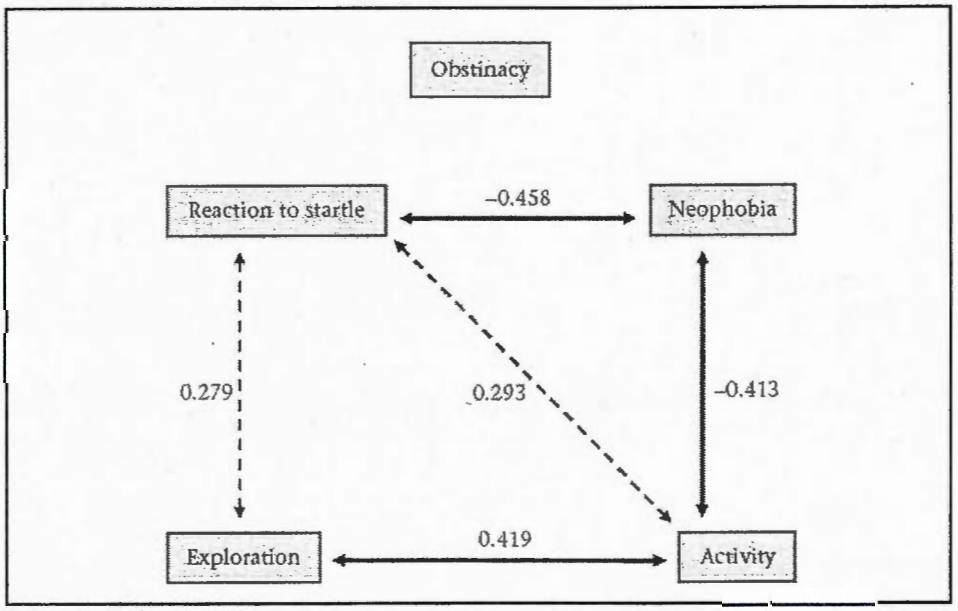

Figure 2.1. Relationships between personality traits defining the behavioural syndrome in our population. Black arrows indicate correlations remaining significant after Benjamini & Hochberg (1995)'s correction (see *Methods* section), whereas dashed arrows indicate marginally significant correlations ($0.05 < P < 0.10$). Pearson's correlation coefficients are indicated above each link.

Behaviour pairs	Pearson r	P
Activity – reaction to startle	0.29	0.063
Activity – exploration	0.42	0.006*
Activity – neophobia	−0.41	0.007*
Activity – obstinacy	0.11	0.481
Exploration – reaction to startle	0.28	0.077
Exploration – neophobia	0.23	0.146
Exploration – obstinacy	0.07	0.657
Neophobia – reaction to startle	−0.46	0.003*
Neophobia – obstinacy	0.22	0.165
Reaction to startle – obstinacy	0.17	0.292

Table 2.1. Correlations between each personality trait. Asterisks indicate correlations remaining significant after Benjamini & Hochberg (1995)'s correction (black arrows in figure 2.1.).

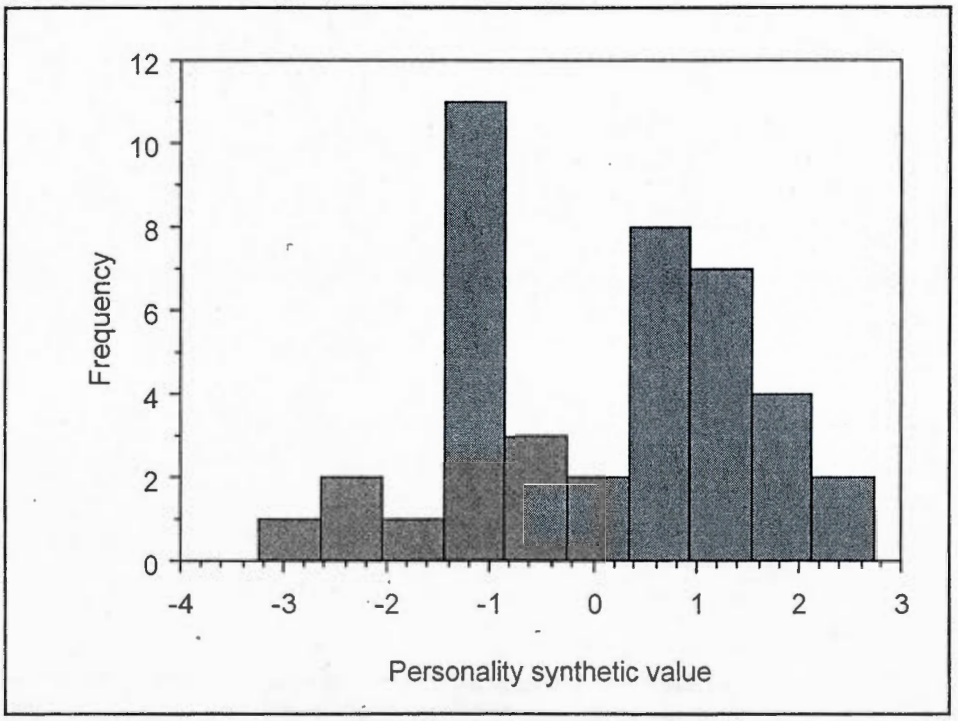

Figure 2.2. Frequency distribution of the personality synthetic values in our sample.

2.4.2. Influence of Personality on Aggressiveness and Social Dominance

The medians for the personality synthetic value did not differ significantly between all constituted groups ($\chi^2_6 = 8.43$, $P = 0.208$), and variances were homogeneous (Levene's test: $F_{6,34} = 1.63$, $P = 0.169$). Ring colour had no effect on access order to feeder ($\chi^2_5 = 2.07$, $N = 41$, $P = 0.840$), initiated aggressive acts ($\chi^2_5 = 4.56$, $P = 0.472$), received aggressive acts ($\chi^2_5 = 4.29$, $P = 0.508$), number of times at the feeder ($\chi^2_5 = 3.53$, $P = 0.620$) nor on total time spent feeding ($\chi^2_5 = 3.61$, $P = 0.606$). Traits defining dominance were highly consistent between trials (access order to feeder: $R = 0.61$, $F_{40,75} = 4.11$, $P < 0.0001$; total time spent feeding: $R = 0.41$, $F_{40,75} = 2.39$, $P = 0.005$; number of given aggressive acts: $R = 0.53$, $F_{40,75} = 3.28$, $P = 0.0003$; number of times at the feeder: $R = 0.65$, $F_{40,75} = 4.76$, $P < 0.0001$). The personality synthetic value moderately but significantly predicted access order to feeder ($R^2 = 0.13$, $N = 41$, $P = 0.021$, figure 2.3.), total time spent feeding ($R^2 = 0.20$, $N = 41$, $P = 0.004$, figure 2.4.), number of times at the feeder ($R^2 = 0.12$, $N = 41$, $P = 0.027$), but not initiated aggressive acts ($R^2 = 0.03$, $N = 41$, $P = 0.251$). Hence, proactive females were more likely to be dominant. Taking each of the seven groups of six birds separately, we observed the same trends in four groups for the relationship between access order to feeder and personality, in six groups for the total time spent feeding, and in five groups for the number of times at the feeder. To assess again the overall consistency of the individual groups separately, the same trends were observed in four groups out of seven for the relationship between access order to feeder and personality, in six groups out of seven for the total time spent feeding, and in five groups out of seven relationship, we combined probabilities from a series of separate Spearman's correlation tests performed within each group (Sokal & Rohlf 1995). Both "time spent feeding" and "number of times at the feeder" were significantly related to the personality synthetic value ($P = 0.048$ for both, one-tailed tests), whereas "order access to the feeder" was not ($P = 0.200$).

Body condition had no effect on access order to feeder ($R^2 = 0.003$, $N = 41$, P

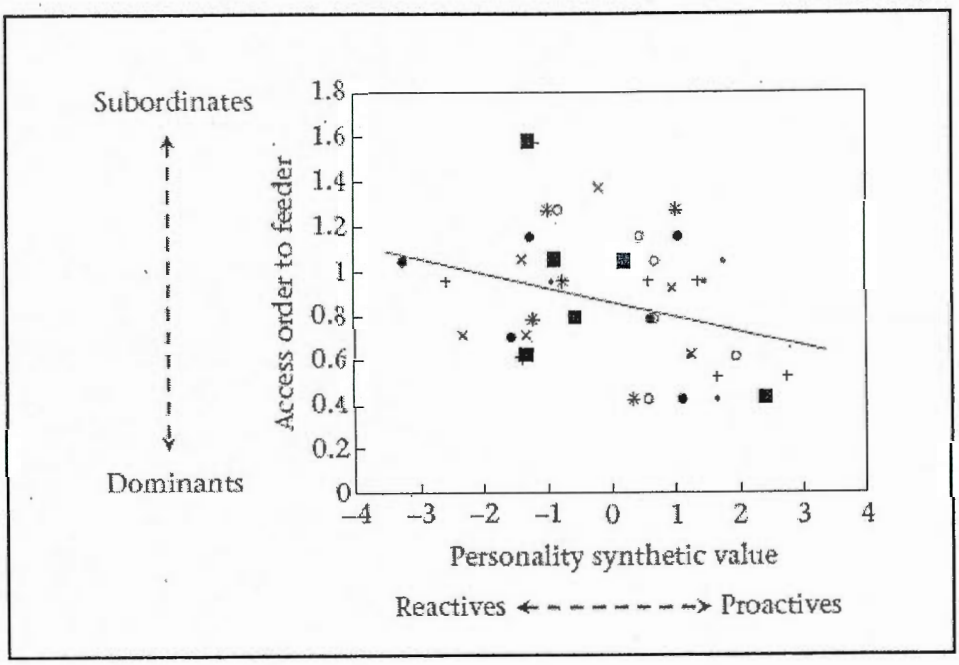

Figure 2.3. Influence of personality on access order to feeder. The y-axis was arcsine-square-root-transformed to reach normality. Personality synthetic value was obtained through a PCA on activity, exploration, reaction to startle and neophobic behaviours. Each symbol corresponds to individuals coming from the same group. Proactive females are more likely to be dominant and reactive ones subordinate.

= 0.733), total time spent feeding ($R^2 = 0.005$, $N = 41$, $P = 0.666$), number of times at the feeder ($R^2 = 0.002$, $N = 41$, $P = 0.806$), initiated aggressive acts ($R^2 = 0.001$, $N = 41$, $P = 0.869$), nor personality synthetic value ($R^2 < 0.001$, $N = 41$, $P = 0.986$).

2.5. DISCUSSION

Four personality traits out of five were correlated within a wide behavioural syndrome in the present study, and proactive individuals were more likely to be

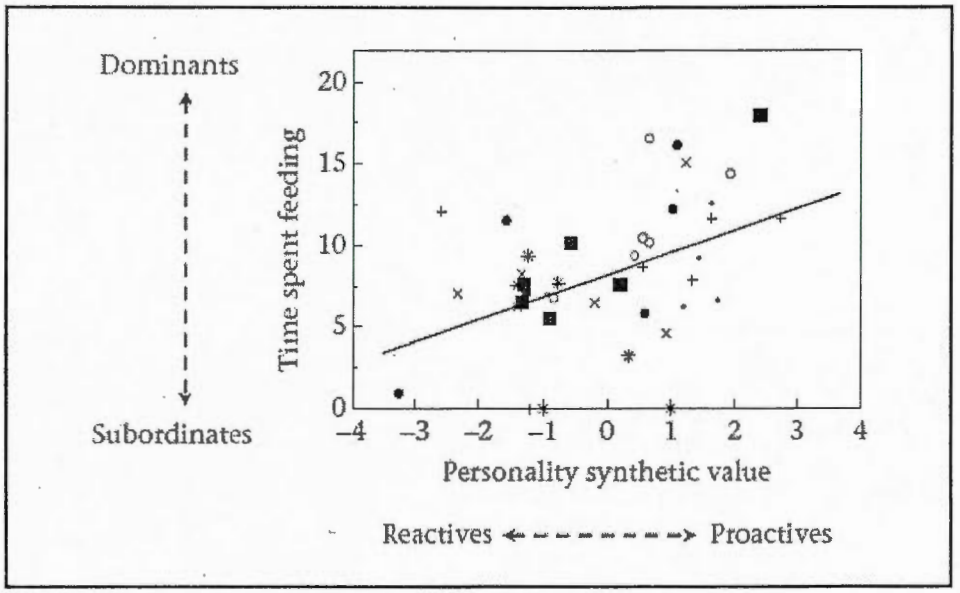

Figure 2.4. Influence of personality on total time spent feeding. The y-axis was square-root-transformed to reach normality. The personality synthetic value was obtained through a PCA on activity, exploration, reaction to startle and neophobic behaviours. Each symbol corresponds to individuals coming from the same group. Proactive females spent more time feeding during the 15-minute trial than reactive ones.

dominant during within-group competition. Although some relationships were only marginally significant, neophobia, activity, exploration and reaction to startle showed substantial correlations, enabling us to sort individuals on a continuum from proactive (explorative, quicker to resume foraging, less neophobic and active birds) to reactive ones (less explorative, longer to resume foraging, neophobic and less active birds). However, one trait, obstinacy, defined as the intensity of escape behaviour in a stressful and threatening situation, was not related to any other. Although we may have a priori expected that such a behavioural reaction would be related to the other traits, with obstinate individuals being quicker to resume foraging and more active for instance, this was clearly not the case. Even though the consequences of obstinacy in terms of survival have never been experimentally challenged, there is little doubt that

the expressed escape behaviour has important consequences, as an anti-predator behaviour or in an intra-specific competition context. This suggests that its measurement is both meaningful and relevant when investigating personality, especially when it could not have been predicted by the other traits, as is the case in our study. Taken together, those statements argue in favour of the need to assess a wide range of traits to provide a full account of individual personality, as it is commonly done in humans (Paunonen et al. 2003; Ashton & Lee 2007; de Vries et al. 2009).

Personality has already been found influencing many components of individual behaviour such as learning (Boogert et al. 2006), mating (Wilson et al. 2010a) or anti-predator behaviour (Jones & Godin 2010). In this study we showed that personality predicted social dominance in a feeding context, a strong predictor of fitness in gregarious bird species (Schubert et al. 2008; see however Verhulst & Salomons 2004). Hence, proactive individuals were more likely to be dominants and spent more time feeding whereas reactive ones tended to be subordinates. Although we only used females in our experiment, we would not expect to obtain different results in mixed or male groups as zebra finches are not territorial but gregarious birds (Zann 1996). We then expect dominance to be mainly beneficial during competition by interference for food in flocks, irrespective of the sex of the birds involved. In addition, it can be observed that both male and female groups show substantial level of between-individual aggressiveness (Adkins-Regan & Robinson 1993; M. David, unpublished data).

Our results make sense in relation to the "life-history productivity" hypothesis (Biro & Stamps 2008), according to which proactive individuals express behaviours enabling them to sustain a high productivity, associated to a high metabolic rate (Careau et al. 2008). It follows that proactivity should be related to a preferential access to feeding resources, which can be achieved through dominance. In this study, subordinate birds, could have reached the feeder after dominant ones, but this was not systematically the case. This suggests that the fact that subordinates spent less time

feeding most likely resulted from lower energetic needs rather than from the monopolization of resources by dominants.

Although similar results were found in a population of great tits (Dingemanse & de Goede 2004), the direction of the relationship between personality and dominance seems to vary between studies and across species. Whereas proactive birds were found to be dominant in the present study, the opposite was observed in a population of mountain chickadees (*Poecile gambeli*) (Fox et al. 2009), and in another study on great tits (Verbeek et al. 1999). Those results lead to the question of why personality consequences on dominance vary across studies. One possibility is that the relationship between the two variables is context-dependent, even within a single population (Dingemanse & de Goede 2004). External factors such as the social organization or the ecology of the species may also explain why individuals of the same personality do not get the same dominance status across species. For instance, Dingemanse & de Goede (2004) argued that territoriality mediated the relationship in a complex way. Consequences of personality are likely to differ as a function of the way individuals compete for food or territory. Unfortunately, few studies investigated the relationship between personality and competition outcomes (but see Höjesjö et al. 2004). However, one could expect proactive individuals to outcompete reactive ones, especially when the intensity of competition by interaction is high. On the other hand, reactive individuals should not get lower success when competition is low, all other things being equal. These simple predictions have the benefit to provide theoretical ground for both intra- and inter-specific studies, as well as ultimately bring insights into how competition may play a role in the differential success of personalities. Finally, the relationship between personality and dominance has been shown to fluctuate among species (Fox et al. 2009; the present study). Such discrepancies offer interesting opportunities to understand which role the ecology of a given species can play in the processes leading to the establishment of within-group dominance hierarchies.

Overall, our study suggests a multi-factorial origin of dominance relationships in zebra finches. Dominance hierarchies are commonly considered as being determined by either individual abilities ("prior attributes" hypothesis) or social interaction between group members ("social dynamics" hypothesis) (Chase et al. 2002). While one process may be predominant over the other, as in cleaning gobies (*Elacatinus prochilos*) (Whiteman & Côté 2004), evidence shows that both may contribute to the establishment of hierarchies (Chase et al. 2002; Valderrábano-Ibarra et al. 2007), which is likely to be the case in our study. Our results indicate that variation in personality explains 13 % of total variation in dominance status in our zebra finch population. If we consider that dominance is determined by both "prior attributes" and "social dynamics", it means that personality (a "prior attribute") explains more than 13 % of variation explained by static factors only, making of it an important predictor of dominance in our biological model. Future research may address the importance of individual personality in shaping hierarchies within groups, through comparing species with contrasted social organizations.

2.6. ACKNOWLEDGEMENTS

We thank Sébastien Motreuil for his assistance during bird care and the building of experimental devices, Elise Melloul for assistance during the experiments and two anonymous reviewers who helped to improve the manuscript. This work was funded with a PhD grant to M.D. and a master honorific grant to Y.A., both provided by the Conseil Régional de Bourgogne.

ARTICLE II

HANDLING STRESS DOES NOT REFLECT PERSONALITY IN FEMALE ZEBRA FINCHES (*TAENIOPYGIA GUTTATA*)

Morgan David, Yannick Auclair, François-Xavier Dechaume-Moncharmont & Frank Cézilly

Journal of Comparative Psychology *in press*

3.1. ABSTRACT

Although increasing attention is given to both the causes and consequences of variation in animal personality, the measurement of personality in captive or free-ranging individuals remains an issue. In particular, one important question concerns whether personality should be established from the existence of complex behavioural syndromes (a suite of correlated behavioural traits), or could be more easily deduced from a single variable. In that context, it has recently been suggested that handling stress, measured through breathing rate during handling, could be a good descriptor of personality, at least in passerine birds. We experimentally investigated to what extent handling stress was correlated with personality in female zebra finches, as assessed from a suite of repeatable behavioural traits including activity, exploratory behaviour, neophobia, and reaction to startle. Although breathing rate was repeatable across individuals, it was not related to any behavioural trait, suggesting that it cannot be used to quickly predict personality, at least in zebra finches. Breathing rate during handling, in addition, was related to morphology, questioning the fact that breathing rate during handling reflects personality irrespective of individual state. We suggest that inference on global personality from a reduced number of traits should be performed with caution.

Keywords: behavioural syndrome, temperament, breathing rate, exploration, bootstrap

3.2. INTRODUCTION

Inter-individual differences in behaviour (so-called "personalities") have recently become of prime interest to ornithologists and behavioural ecologists (Réale, Reader, Sol, McDougall & Dingemanse, 2007). Indeed, recent evidence shows that personality traits, such as neophobic or exploratory tendencies, can have fitness consequences (Smith & Blumstein, 2008) and can evolve through natural (Quinn, Patrick, Bouwhuis, Wilkin & Sheldon, 2009) and sexual selection (Schuett, Tregenza & Dall, 2010). Interestingly, some personality traits can be found to be related to each other at the population level, thus forming a "behavioural syndrome" (Wilson et al., 2010). These correlations have several implications for behavioural studies. First, they suggest that different behaviours do not evolve independently but act as constraints towards each other, setting the stage for an integrative study of behaviour (Sih, Bell & Johnson, 2004a). Second, these correlations, once established, can potentially enable experimenters to assess only a reduced number of traits to determine individual global personality (Fucikova, Drent, Smits & van Oers, 2009). For instance, in great tits (*Parus major*), breathing rate after handling has been related to both exploratory tendencies and neophobia, and used as an indicator of individual personality (Carere & van Oers, 2004, Fucikova et al., 2009). Exploratory birds had a higher breathing rate during handling (Fucikova et al., 2009), while bold individuals had a lower breathing rate (Carere & van Oers, 2004). These results suggest that breathing rate after handling might be used a proxy for personality in other bird species, given its ease of measurement in both field and lab conditions. Recent evidence, however, suggests that the assessment of personality may not always be reduced to the measurement of one single behavioural trait. For instance, David, Auclair & Cézilly (2011a) found that although neophobia, exploratory tendencies, activity, and reaction to a startle were related to each other within a broad behavioural syndrome in zebra finches (*Taeniopygia guttata*), obstinacy, while showing very high repeatability (i.e. within-individual consistency through time), was not related to any

other personality trait (David et al., 2011a). The use of a quickly assessable trait, such as breathing rate after handling, as a general proxy for personality in bird species then deserves further consideration. Therefore, following Fucikova et al. (2009), we investigated to what extent breathing rate following handling can predict personality in the zebra finch, while controlling for the effect of body mass and body condition on handling stress.

3.3. METHODS

3.3.1. Study subjects

Forty-one wild-type female zebra finches, in which personality had been assessed in a previous study (David et al., 2011a), were kept in home cages (60 × 30 × 33 cm), by unisex groups of two or three birds, before the experiments. Zebra finches are small monogamous and gregarious passerine birds, widely used in behaviour studies (Zann, 1996). Each individual was identified with an orange numbered ring (AC Hughes, Hampton Hill, UK; size XF). Only females were used, as the present study was part of a larger research program on the influence of personality on female sexual behaviour. Our captive stock was kept in a breeding room where temperature was maintained at 22±2°C and the photoperiod was 13:11h light:dark cycle (0730am-0830pm). Birds were provisioned with millet seeds, cuttlebones and water *ad libitum*. At the end of the experiment, birds were kept in groups of two to be used in subsequent studies. The experimental procedures were in agreement with the ethical requirements of the Université de Bourgogne.

3.3.2. Assessment of personality traits

Birds were food-deprived for one hour before each trial to control for hunger levels. All tests were performed on individuals kept single. Activity corresponded to the

number of movements performed in the home cage during a 10-minute period. Neophobia was assessed from the tendency to feed near and to approach a novel object in the home cage. Exploratory tendencies were measured from the number of movements performed in a large unfamiliar cage (140 × 140 cm and 70 cm high) containing five artificial trees, each composed of four small branches. Reaction to a startle corresponded to the latency time to resume foraging in the home cage after a stressful event. All these personality traits have been found to be highly repeatable in zebra finches in a previous study (David et al., 2011a). Detailed information concerning experimental apparatus and methodology can be found in David et al. (2011a).

3.3.3. Handling stress

Following previous studies conducted on small passerines (Carere & van Oers, 2004, Fucikova et al., 2009), we assessed handling stress from the intensity of breathing rate after being caught by an experimenter. All birds were kept single in their home cage. One experimenter (Y.A.) caught each bird in its own home cage, and measured the number of breast movements during 20 seconds as a measure of breathing rate (see Carere et al., 2001), while handling the bird on the back. Catching latency was also quantified as the latency time to catch the bird within its home cage. This procedure was repeated two times a one-week interval and both measures were averaged for each individual. All trials were performed at the same time of the day (6:00pm) for all individuals in order to discard the potential effect of diurnal variation in behavioural activity or stress response. The first handling stress trial was conducted one day before personality tests began.

3.3.4. Morphometric measures

All morphometric measures were taken twice on two different days by Y.A and two days before starting personality tests. Tarsus length was measured with a digital calliper to the nearest 0.1 mm. Birds were weighed to the nearest 0.01 g with an electronic balance (Ohaus, Scout Pro SPU202) at the same time of day for each individuals. Values were then averaged for each bird. We determined body condition through the residuals calculated from the linear regression of $\log_{10}$(body mass) on $\log_{10}$(tarsus length) (Schamber, Esler & Flint, 2009).

3.3.5. Statistical analyses

Consistency (R) of catching latency and breathing rate were assessed through Lessells & Boag's (1987) method. Differences between both handling trials were assessed through paired t-tests, followed by the calculation of Cohen's d as a measure of effect size (Nakagawa & Cuthill, 2007). Statistics are reported with mean or R and 95% Confidence Interval (CI; Nakagawa & Schielzeth, 2010). Relationships between personality and breathing rate were tested using Pearson's correlations. All statistical analyses were performed with JMP 5.0.1 (SAS Institute, Cary, NC).

3.4. RESULTS

Overall, all measured behaviours were repeatable. However, whereas breathing rate was found to be related to body mass or catching latency, no relationship was found between breathing rate and any of the personality traits:

Mean catching latency was 6.8 ± 0.6 sec (mean ± 95% CI; $n = 41$). Catching latency and breathing rate were repeatable across both trials (catching latency: $R = 0.31$, 95% CI [0.02; 0.60], $F(40, 81) = 1.90$, $p = 0.02$; breathing rate: $R = 0.66$, 95% CI [0.47; 0.84], $F(40, 81) = 4.80$, $p < 0.0001$). Catching latency moderately predicted

breathing rate during the first trial ($R^2 = 0.14$, bootstrap 95% CI [<0.01; 0.37], $F(1, 40) = 5.52$, $p = 0.02$), but not during the second one ($R^2 = 0.04$, bootstrap 95% CI [<0.01; 0.19], $F(1, 40) < 0.01$, $p = 0.99$). However, overall, variation in breathing rate in relation to catching latency did not differ between the two trials (analysis of covariance, $F(2, 40) = 1.88$, $p = 0.17$). Catching latency did not differ between trials ($t(1, 40) = -0.37$, $p = 0.71$, $d = -0.07$), whereas breathing rate slightly increased from 66.2 (95% CI [64.5; 67.9]) to 67.9 (95% CI [66.0; 69.7]) breast movements between trials ($t(40) = 2.37$, $p = 0.02$, $d = 0.04$). The influence of personality on breathing rate was thus analyzed after pooling data from the two trials or considering each trial separately.

Average breathing rate was moderately predicted by body mass ($R^2 = 0.12$, bootstrap 95% CI [<0.01; 0.32], $F(1, 40) = 4.49$, $p = 0.04$), but not by body condition ($R^2 = 0.04$, bootstrap 95% CI [<0.01; 0.20], $F(1, 40) = 0.88$, $p = 0.35$). Heavier individuals showed a higher breathing rate after handling. However, catching latency was not influenced by body mass ($R^2 = 0.04$, bootstrap 95% CI [<0.01; 0.18], $F(1, 40) = 1.06$, $p = 0.31$) or body condition ($R^2 = 0.09$, bootstrap 95% CI [<0.01; 0.26], $F(1, 40) = 3.40$, $p = 0.07$). We then computed the variables "breathing rate adjusted for catching latency" and "breathing rate adjusted for body mass" by calculating the residuals from the regressions of breathing rate on catching latency and breathing rate on body mass. None of the four personality traits was significantly related to breathing rate, breathing rate adjusted for mass or for catching latency when considering the two trials separately (Table 3.1.). In addition, none of the four personality traits was significantly related to breathing rate adjusted for mass averaged across the two trials (activity: $r(39) = -0.12$, 95% CI [-0.41; 0.19], $p = 0.45$; reaction to startle: $r(39) = 0.06$, 95% CI [-0.25; 0.36], $p = 0.72$; exploration: $r(39) = -0.09$, 95% CI [-0.39; 0.22], $p = 0.56$; neophobia: $r(39) = -0.16$, 95% CI [-0.45; 0.15], $p = 0.31$; Figure 3.1.).

Variable	Exploration		Activity		Neophobia		Reaction to startle	
	r (95% CI)	*p*	*r* (95% CI)	*p*	*r* (95% CI)	*p*	*r* (95% CI)	*p*
Breathing rate								
1st trial	−0.17 (−0.45, 0.15)	0.29	−0.11 (−0.40, 0.21)	0.51	−0.16 (−0.45, 0.15)	0.31	0.17 (−0.14,0.46)	0.28
2nd trial	−0.11 (−0.40, 0.20)	0.49	−0.06 (−0.36, 0.25)	0.70	−0.16 (−0.45, 0.15)	0.31	0.10 (−0.22, 0.39)	0.54
Breathing rate adjusted for mass								
1st trial	−0.13 (−0.42, 0.18)	0.42	−0.13 (−0.42, 0.19)	0.43	−0.15 (−0.44, 0.16)	0.34	0.12 (−0.20, 0.41)	0.47
2nd trial	−0.04 (−0.34, 0.27)	0.80	−0.10 (−0.39, 0.22)	0.54	−0.15 (−0.44, 0.17)	0.35	<0.01 (−0.31, 0.30)	0.96
Breathing rate adjusted for catching latency								
1st trial	−0.15 (−0.44, 0.17)	0.36	0.02 (−0.29, 0.33)	0.90	−0.02 (−0.32, 0.29)	0.89	0.08 (−0.24, 0.38)	0.64
2nd trial	−0.11 (−0.40, 0.20)	0.49	−0.06 (−0.36, 0.25)	0.70	−0.16 (−0.45, 0.15)	0.31	0.10 (−0.22, 0.39)	0.54

Note. CI = confidence interval. Breathing rate adjusted for mass and adjusted for catching latency was computed as the residuals of the linear regression of breathing rate on respectively body mass and catching latency. Degrees of freedom equal 40 for each test.

Table 3.1. Relationships between each personality trait and breathing rate, breathing rate adjusted for mass, and for catching latency. Breathing rate adjusted for mass and adjusted for catching latency was computed as the residuals of the linear regression of breathing rate on respectively body mass and catching latency. Degrees of freedom equal 40 for each test.

3.5. DISCUSSION

The present study investigated whether breathing rate during handling can be a reliable predictor of personality in zebra finches. Response to handling stress in the form of breathing rate was found to be consistent within individuals. However, our results indicate that individual variation in response to handling stress is not associated to individual variation in personality in female zebra finches, as least as assessed from the methodology used in David et al. (2011a), thus casting doubts on the extent to which response to handling stress should be used as a proxy to assess personality.

In particular, we found no evidence for a relationship between exploratory tendency or neophobia and breathing rate, contrary to what has been previously

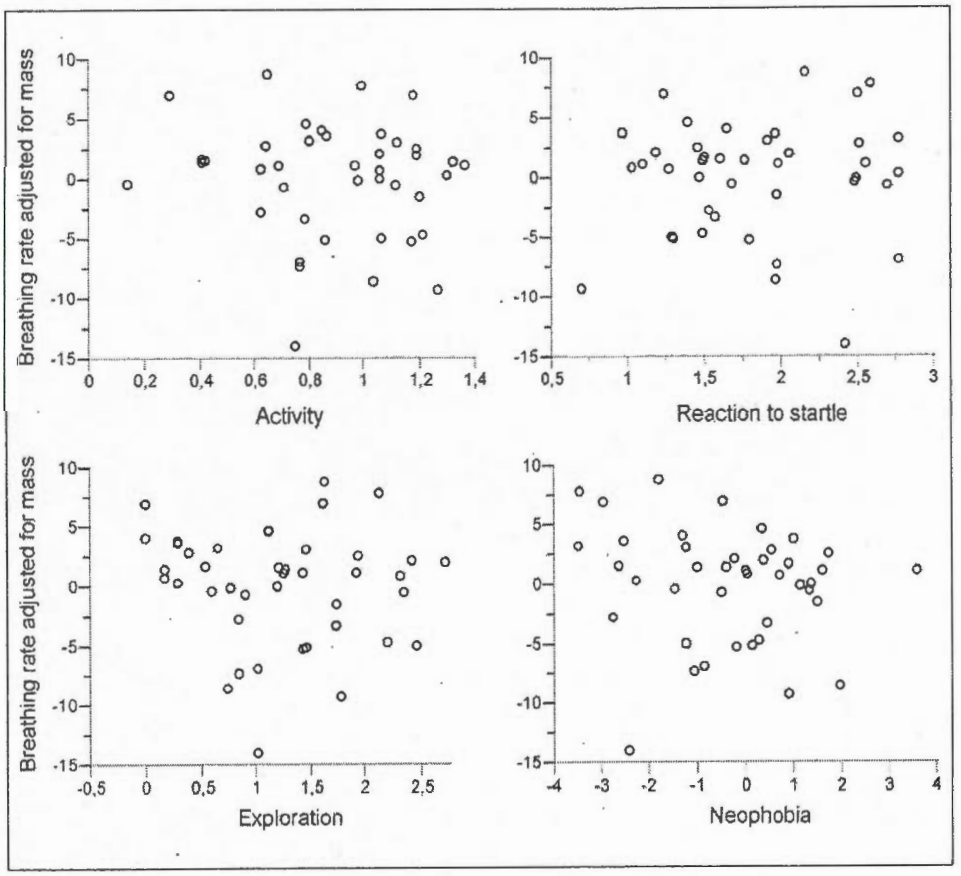

Fig. 3.1. Non-significant relationship between each personality trait and breathing rate (averaged across the two trials) adjusted for mass during handling. Breathing rate adjusted for mass was computed as the residuals of the linear regression of breathing rate on body mass.

reported in great tits (Carere & van Oers, 2004, Fucikova et al., 2009). The same was true of two other different personality traits, activity and reaction to startle. In addition, contrary to what was observed in great tits (Carere & van Oers, 2004), we found that breathing rate was positively correlated with body mass in female zebra finches, such that heavier individuals had a higher breathing rate during handling. This might be explained by the tight relationship between metabolism and body mass

(Clarke & Johnston, 1999, McNab, 2002), and by the fact that metabolic rate depends on oxygen consumption and is directly related to ventilation rate in passerines (Arens & Cooper, 2005). The absence of a relationship between personality and breathing rate is particularly interesting as some evidence suggests that basal metabolic rate is heritable in zebra finches (Rønning, Moe & Bech, 2005). Indeed, personality traits are supposed to be independent from any motivational or life-history state (Réale et al., 2007), although few studies verified this assumption so far (Fucikova et al., 2009).

Several explanations, based on methodological issues or biological differences between species, can however be advanced to explain the observed discrepancy between our results and those obtained in great tits (Carere & van Oers, 2004, Fucikova et al., 2009). From a methodological point of view, the present study only used females as study subjects. The possibility then remains that breathing rate is related to male personality but not to female one, although this seems unlikely. In addition, Carere & van Oers (2004) estimated breathing rate in great tits during a 60-second period, which is substantially longer than in the present study. Nonetheless, we believe that this discrepancy cannot be responsible for the results we obtained, as zebra finches get stressed from both human presence and catching. Breathing rate is thus likely to reflect a stable stress state in our experiment rather than the escalation of stress. Finally, Carere & van Oers (2004) assessed individual personality only from reaction of birds towards a novel object. Because animal personality is most probably composed of several dimensions, it might be difficult in practice to assess it from one single trait, and inference of this sort should then be performed with extreme caution in future studies. For instance, in zebra finches, social dominance within groups is influenced by a set of personality traits such as exploration or activity (David et al., 2011a). Conversely, obstinacy, which is not related to other personality traits but shows high repeatability, has no effect on social dominance in this species (David et al., 2011a).

Another possibility is that the relationship between personality and physiological traits may vary between species. Great tits are obligate cavity nesters, usually nesting in a hole in a tree, whereas zebra finches are not (Zann, 1996; see however Griffith, Pryke & Mariette, 2008). Some evidence suggests that chronic exposition to CO2 during development may affect the development of ventilatory behaviour in cavity-nesting bird species (Williams & Kilgore, 1992), eventually affecting the observed relationship personality and breathing rate in adult birds. Whatever the causes of observed discrepancies between studies, additional work is clearly needed to assess the extent to which breathing rate can be used as a reliable proxy for overall personality in great tits and other species.

3.6. ACKNOWLEDGMENTS

We thank Vincent Careau for his advice on bird metabolism, Sébastien Motreuil for assistance during bird care and the building of experimental devices, and Elise Melloul for assistance during the experiments. We thank three anonymous referees for their valuable comments which help to improve the manuscript. This work was funded with a PhD grant to M.D. and a master honorific grant to Y.A., both provided by the Conseil Régional de Bourgogne.

ARTICLE III

PERSONALITY MAY CONFOUND COMMON MEASURES OF MATE-CHOICE

Morgan David & Frank Cézilly

PLoS ONE 6(9), e24778

4.1. ABSTRACT

The measurement of female mating preferences is central to the study of the evolution of male ornaments. Although several different methods have been developed to assess sexual preference in some standardized way, the most commonly used procedure consists of recording female spatial association with different males presented simultaneously. Sexual preference is then inferred from time spent in front of each male. The extent to which the measurement of female mate choice is related to exploration tendencies has however not been addressed so far. In the present study we assessed the influence of variation in exploration tendencies, a trait closely associated to global personality, on the measurement of female mating preference in the zebra finch (*Taeniopygia guttata*) using the widely used four-chamber choice-apparatus. The number of movements performed within both exploration and mate-choice apparatus was consistent within and across the two contexts. In addition, personality explained variation in selectivity, preference strength and consistency. High-exploratory females showed lower selectivity, lower preference scores and displayed more consistent preference scores. Our results suggest that variation in personality may affect the measurement of female mating preference and may contribute to explain existing inconsistencies across studies.

Keywords: selectivity; sexual preference; choosiness; exploration; repeatability, mate sampling

4.2. INTRODUCTION

Assessing female mating preferences is of central importance in the understanding of the evolution of male ornaments through inter-sexual selection (Andersson, 1994). Despite extensive empirical effort (Andersson & Simmons, 2006; Jones & Ratterman, 2009), mating preference remains one of the least repeatable behavioral trait (Bell *et al.*, 2009). Yet, several different experimental techniques have been developed to assess female preference in a vast array of taxa (Wagner, 1998). Although experiments in the field can be carried out to infer female choice (Chaine & Lyon, 1998), investigations conducted on captive animals are generally considered to allow for a better control of experimental conditions such as female motivation or male density. Female preference may then be deduced from observing the formation of sexual pairs between individuals interacting freely in a controlled environment (Rutstein *et al.*, 2007), or from the female's willingness to copulate with different males presented sequentially (Shackleton *et al.*, 2005; Narraway *et al.*, 2010). However, mate choice inferred from spatial association is the most commonly used procedure (Wagner, 1998). This method consists of recording the time spent with or the number of times in front of different males simultaneously presented to the female in different small and visually isolated enclosures (Woodgate *et al.*, 2010). All three techniques enable to link male characteristics to female sexual preference, or at least to female choice (but see Heisler *et al.*, 1987), and to estimate the intensity of sexual selection pressures potentially acting on male traits (Hunt *et al.*, 2009). However, studies conducted on individuals from the same species commonly highlight variation between females in their sexual preference (Collins & Ten Cate, 1996; Brooks & Endler, 2001). Furthermore, inherent technical limitations remain. For instance, in spatial association tests, the measurement of female preference and selectivity is inferred from individual position within the apparatus over the course of the trial. This suggests that these measures can be dependent upon female activity or locomotor behavior during tests.

Although inter-individual differences in activity and exploratory behavior are common within species (see Smith & Blumstein (2008) and references therein) and are often included in the characterization of personality syndromes (Dingemanse *et al.*, 2007; David *et al.*, 2011a), their relationship with mating behavior remains poorly investigated (but see Schuett *et al.* (2010). Few studies have up to now examined the extent to which personality variation may underlie variation in mate-choice (Schuett *et al.*, in press). More specifically, the influence of exploration tendencies on the measurement of female mating preference has not been addressed so far, and the possibility remains that preference and selectivity reflect female spatial activity within the mate-choice apparatus.

In the present study we address this issue by testing the influence of exploration tendencies on the measurement of selectivity and preference during mate-choice trials through spatial association. We used the dimorphic zebra finch, *Taeniopygia guttata*, which is a model species for studies of sexual selection and personality (Rutstein *et al.*, 2007; David *et al.*, 2011a). We first assessed exploration tendencies of females in a standard test cage with which birds were unfamiliar (Dingemanse *et al.*, 2002; David *et al.*, 2011a; David *et al.*, in press). Female choice was then tested in a four-chamber apparatus, a device regularly used to assess female sexual preference in zebra finches (Forstmeier & Birkhead, 2004; Woodgate *et al.*, 2010), and more generally, in vertebrates (Pearn *et al.*, 2001; Hohoff *et al.*, 2003).

4.3. MATERIALS AND METHODS

4.3.1. Study subjects

Twenty-eight females and 42 males were purchased from a reliable supplier (Girardot, 21 Tichey, France) and, to avoid any stress due to isolation in this gregarious species, were maintained in a single room where all manipulations were performed. Only individuals with wild-type phenotypes were used in this experiment.

All individuals were sexually experienced (i.e. underwent mate-choice trials and staged encounters with males during a previous study), to avoid the problem that females are less selective or less responsive when courted for the first time in their life (Fortsmeier, 2004, 2007). Birds were kept in unisex groups of two to three individuals in home cages (65 ×33 ×35 cm) containing four perches and four feeders. Room temperature was maintained at 22±2°C and the photoperiod was 13:11h light:dark (0730–2030 hours), with a 30-minute period of increasing light intensity in the morning and decreasing light intensity in the evening to imitate dawn and dusk. Each individual was identified by an orange plastic numbered ring (A.C. Hughes, Hampton Hill, U.K.; size XF), a neutral colour regarding male attractiveness (Burley *et al.*, 1982). Birds were provided with millet seeds, cuttlebones and water ad libitum. At the end of the experiment, birds were kept in groups of two to be used in subsequent studies. According to the "Decree No. 87-848 of October 19, 1987 relatif aux expériences pratiquées sur les animaux vertébrés" on experiments involving vertebrate animals, no specific ethical approval is necessary for this type of study as it is a non-invasive observational study. Treatment of animals complied with this law and with the Université de Bourgogne's requirements concerning animal ethics.

4.3.2. Assessment of exploration tendencies

Exploration tests were inspired by the classic procedure used in bird personality studies (Dingemanse *et al.*, 2002; David *et al.*, 2011a,b; David *et al.*, in press). Female exploration tendencies were assessed in a large, unfamiliar cage (140 ×140 ×70 cm) with opaque walls, a clear Plexiglas ceiling, and comprising five artificial trees each with four small branches. Neither food nor water was provided to prevent the focal individual to engage in any foraging activity. Before trials, birds were food-deprived for 1 h in a half-home cage, before being introduced in a black box placed against a small sliding door on one side of the apparatus. The experimenters then

gently opened the door with a pulley system from outside the room, causing the focal bird to enter the apparatus. Individual behavior was then recorded during 30 minutes with a video-camera (JVC Everio GZ-MG20) placed one metre above the apparatus. Exploration tendencies were assessed twice with a period of two to four days between trials. During the analysis, the experimenter (MD) recorded the total number of movements between trees and between branches of a single tree. Exploratory tendencies further refer to the cumulative number of movements performed within the apparatus (David *et al.*, 2011a,b).

4.3.3. Mate choice trials

Female mate-choice was assessed in a classic four-chamber choice-apparatus (Fig. 4.1). The central section contained one perch and two feeders containing millet seeds and water ad libitum. One perch in each arm allowed the focal female to stand in front of each stimulus-individual. Each focal female performed three trials on three consecutive days with the same stimuli-individuals, enabling us to assess behavioral consistency. The first trial allowed the birds to acclimatize to the apparatus (Woodgate *et al.*, 2010), and only the second and the third trial were video-recorded and used for data analysis. For each trial, three stimuli-males were randomly assigned to one of the four arms of the apparatus. In addition, one control-female was randomly assigned to one arm to control for focal female's sexual motivation (Pearn *et al.*, 2001; Griggio *et al.*, 2011). The position of stimuli-individuals was also randomized among trials. Birds were given three minutes to acclimatize to the apparatus (Rutstein *et al.*, 2007). This period proved to be sufficient for captive birds to recover from the manipulation (M. David, personal observation). Opaque partitions prevented the focal female to see the other birds during this period. Partitions were then gently removed. Female behavior was video-recorded for 30 minutes with a video-camera placed two metres above the apparatus.

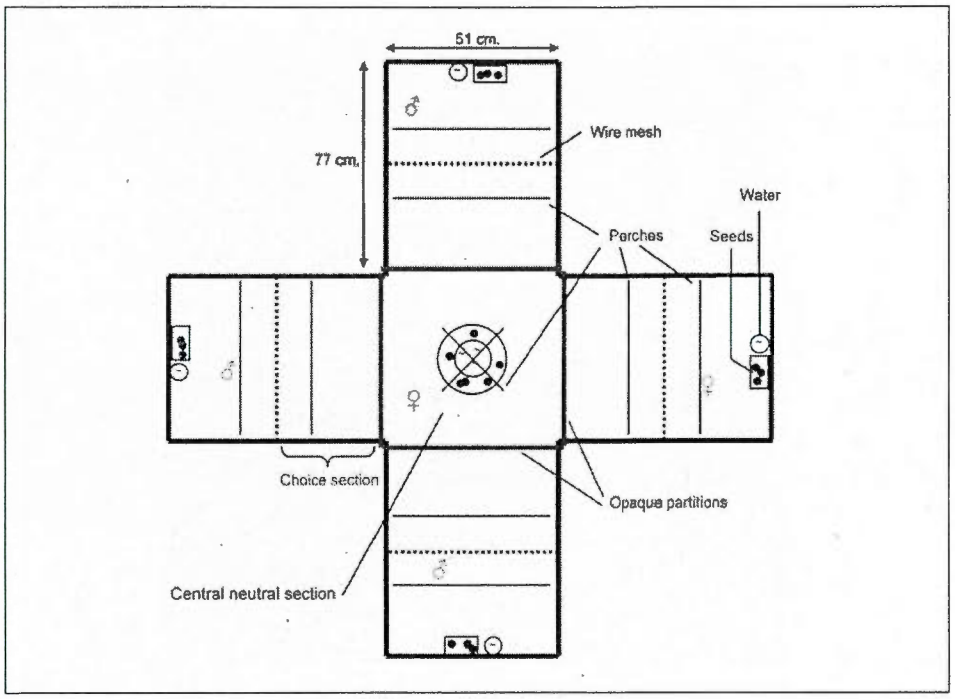

Figure 4.1. Four-chamber choice-apparatus as seen from above.

The first two minutes of recording following the removal of the partitions were discarded from the analysis. Again, this period was largely sufficient for females to recover from the manipulation, i.e. resume any normal activity such as flying or calling. Moreover, stress diminution was greatly facilitated by the other birds' presence. The number of movements performed by the focal individual between each perch of the apparatus was quantified. Focal female position in the apparatus was recorded every ten seconds according to the time sampling method (Martin & Bateson 1993). Each stimulus-male was used six times, i.e three times in front of two different focal females, but within different trios of stimuli-males.

4.3.4. Data analysis

Female preference was defined as the number of times observed near a given male (Rutstein *et al.*, 2007). Thus, for a given focal female, each stimulus-male was assigned a preference score ranging from zero to 180. The male obtaining the highest score during the first recorded trial was considered as the preferred mate for a given focal female. A selectivity index, was defined as the standardized deviation from an egalitarian allocation of time between each stimulus-individual (termed "discrimination" in Forstmeier *et al.* (2004), with

Selectivity index = $(|t_1-0.25| + |t_2-0.25| + |t_3-0.25| + |t_4-0.25|)/4$,

where t_i is the percentage of times observed near stimulus-individual i. The selectivity index varies from 0 to 0.375 with the highest value corresponding to the more selective females (i.e. spending most of their time near a single male). Number of movements within the mate-choice apparatus, preference score for the preferred male, and selectivity index were all individually averaged across the two trials. Hence, "preference score for the preferred male" further refers to the average score across the two trials for the male that has been preferred during the first recorded trial.

We assessed behavioral consistency (R) at the population level using the ANOVA's intra-class correlation coefficient following Lessells & Boag's (1987) method. Individual consistency in preference score was assessed by comparing the score for the preferred male during the first recorded trial and the score for the same male during the second recorded trial. We thus quantified individual consistency by extracting the absolute value of the residuals obtained from the regression of the score obtained during the second trial on that obtained during the first one. Females being more consistent were defined by low values whereas less consistent females obtained high values.

Finally, linear regressions with "number of movements performed in the exploration apparatus" as a predictive variable were carried out to determine the influence of exploration on components of mate-choice. Analyses were all performed

using JMP 5.0.1. statistical software (SAS Institute, Cary, NC, U.S.A.). Only two-tailed tests were used. Data were log or square-root transformed when necessary to reach normality. Sample size was 28 focal females for all analyses.

4.4. RESULTS

4.4.1. Behavioral consistency

Number of movements were significantly repeatable both within the exploration apparatus (mean±95% confidence interval: 27.1±12.7; R=0.45, $F_{27, 55}$=2.63, p=0.007), and the mate-choice apparatus (mean±95% confidence interval: 59.3±25.7; R=0.92, $F_{27, 55}$=24.04, p<0.0001). Preference scores for the preferred male and selectivity indexes were also significantly repeatable across trials (preference scores: R = 0.33, $F_{27, 55}$=1.99, p=0.037; selectivity indexes: R=0.63, $F_{27, 55}$=4.43, p<0.0001). The number of focal females preferring twice the same arm of the apparatus did not differ from the number expected by chance alone (*i.e.* 25%) (χ^2 = 0.615, p > 0.25), thus indicating that females were unlikely to position themselves in relation to any unexpected external cue.

4.4.2. Personality and mate-choice

The number of movements within the exploration apparatus significantly predicted the number of movements performed during mate choice trials (R^2=0.25, $F_{1, 27}$=8.76, p=0.007: Fig. 4.2.), indicating that exploration tendencies were consistent across the two contexts (R=0.50, $F_{27, 55}$=3.01, p=0.003). The number of movements within the exploration apparatus also predicted selectivity index (R^2=0.22, $F_{1, 27}$=7.37, p=0.012; Fig. 4.3.A), preference score for the preferred male (R^2=0.18, $F_{1, 27}$=5.56, p=0.026: Fig. 4.3.B) and preference consistency (R^2=0.17, $F_{1, 27}$=5.31, p=0.029: Fig. 4.3.C).

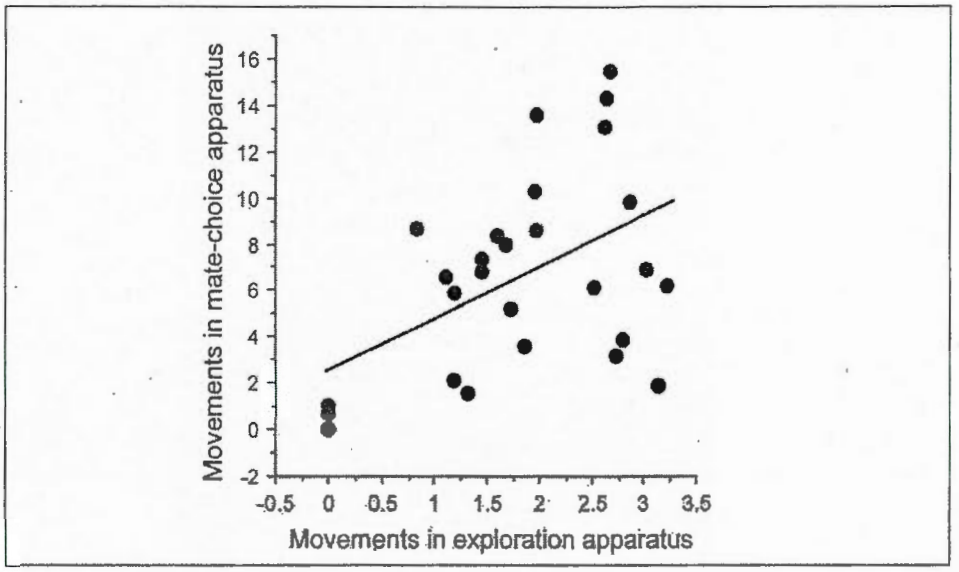

Figure 4.2. Influence of exploration tendencies on the number of movements performed during mate-choice trials. Both scales are transformed to reach normality.

Thus, the more an individual was active within the exploration apparatus, the less it was selective during mate choice, the lower was its preference for the preferred male, but the more this preference was repeatable. Furthermore, selectivity was positively correlated to preference score for the preferred male (Pearson's r: r_{27}=0.48, p=0.010) and negatively related to preference consistency (r_{27}=-0.67, p=0.0001). Finally, time spent in front of control females was not affected by exploration tendencies (R^2<0.01, $F_{1, 27}$=0.03, p=0.85).

4.5. DISCUSSION

The number of movements performed within the exploration apparatus significantly predicted the number of movements performed in the mate-choice apparatus. Our results thus show that consistent variation in exploration tendencies, a trait linked to global personality in several species (Garamszegi *et al.*, 2009; David *et al.*, 2011a),

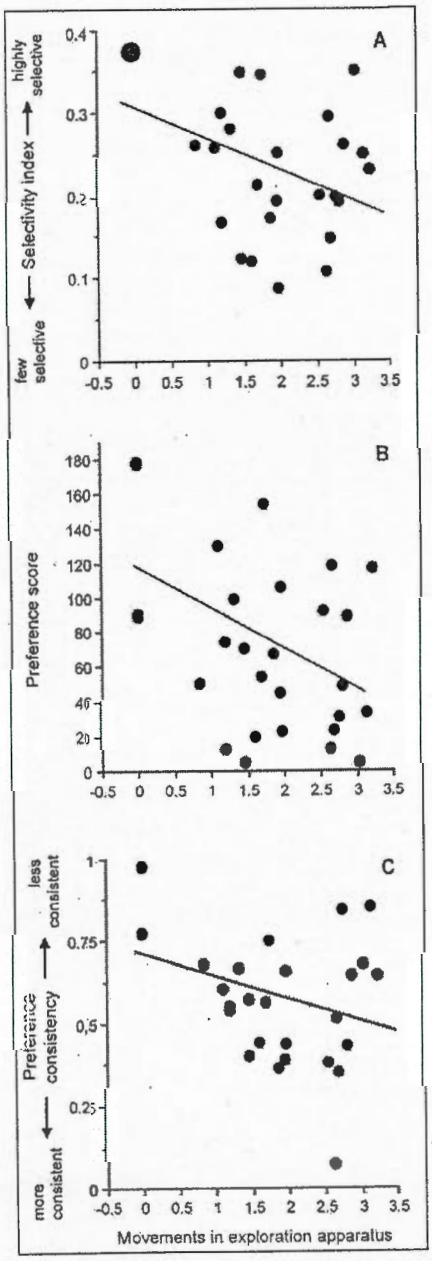

Figure 4.3. Influence of exploration tendencies on mate-choice components: selectivity index (A), mean preference score for the preferred male (B), and preference consistency (C). X-axis scale has been transformed to reach normality.

can affect the measurement of female mate preference. In addition, variation in personality influenced selectivity, preference scores and preference consistency. Exploratory females allocated their time more equally between each stimulus-individual, and showed lower selectivity and lower preference scores for the preferred male, but higher preference repeatability, compared to less exploratory females. Moreover, measures of preference and selectivity were found to be correlated to each other. This result is however not surprising, as both selectivity and preference was calculated from the number of times that focal females were observed in front of each male. Likewise, highly selective individuals are more likely to show consequential variation between the two preference scores as they allocate their time less evenly between stimuli-individuals and thus display higher preference scores.

Our study was not designed, however, to determine female directional preference for a particular male trait such as beak colour (Forstmeier & Birkhead, 2004) or song quality (Ritschard *et al.*, 2010), i.e. males were randomly allocated to trials, with no attempt to maximise phenotypic differences between males within a trial. In addition, the presence of a control female in one arm of the apparatus may have contributed to decrease the contrast between males, and, hence, may have affected selectivity. Yet we found no effect of focal female's personality on time spent near the control-female. On the other hand, females may actually be likely to base their preference on a combination of traits rather than on a single trait (Calkins & Burley, 2003), such that our experimental procedure still provided the possibility that females expressed a preference for a particular male (Head *et al.*, 2005; Narraway *et al.*, 2010). Future studies should then address the influence of variation in female personality on the measurement of female preference in various contexts and with different choice apparatus.

Increasing evidence indicates that variation in personality can explain substantial inter-individual variation in behavioral performance (Réale *et al.*, 2007). More to the point, uncontrolled variation in personality may eventually affect the conclusions of studies in behavior and ecology. For instance, it has been shown that

individuals with different personalities along the shy-bold axis have different trappability in the wild (Biro & Dingemanse, 2009; Garamszegi *et al.*, 2009), with obvious implications for the design of field studies and the analysis of life-history traits from capture-mark-recapture modelling (Clobert, 1995). Similarly, our results suggest that variation in personality may affect the measurement of female mating preference, at least in a classic spatial association setup like a four-chamber apparatus. This indicates that, in some cases, female mating behavior may hardly be distinguishable from her mere propensity to move about in an experimental apparatus. Selectivity and preference scores could simply be understood as artefacts of being more or less exploratory. Future mate choice studies should cautiously consider the possibility that preference estimates might reflect exploration tendencies rather than an exact assessment of the propensity to mate with a given male.

Our results may then have some consequences for the design and interpretation of both experimental and field studies of female mate preference. For instance, it has been shown that differences in rearing conditions may induce variation in personality (Carere *et al.*, 2005). The possibility then exists that studies relying on different stocks of captive birds reared in different environments may differ in their conclusions partly because of differences in personality between groups. This could contribute to explain the recurrent inconsistencies within and between different studies (Collins & Ten Cate, 1996; Bell *et al.*, 2009). In zebra finches for instance, female preference for males with redder beaks, thought to be a signal of quality, is still debated (Collins & Ten Cate, 1996). Results from empirical investigations have thus provided contrasting evidence as whether redder beaks are subject to female preference or not (Collins & Ten Cate, 1996). The possibility then remains that the average exploration tendencies of focal females vary between studies, which could in turn affect the conclusions. For instance, using a majority of exploratory females could lower the average preference scores measured, thus reducing the likelihood to observe a significant relationship between the presumed preferred male trait and female preference. Besides, many studies set a preference

criterion under which focal females are discarded from the sample because of a presumed lack of sexual motivation (Burley & Foster, 2006; Rutstein *et al.*, 2007; Lehtonen & Lindström, 2008). Our results suggest that such data censoring, without any further justification, may lead to biases and non-representative estimates of female preference if females are unintentionally discriminated on the basis of their personality.

Overall, caution should be exerted when inferring female preference from spatial association measured in such experimental setups. The use of mating probability, discrete female choice or copulations might be a more reliable way to assess female mate choice (Forstmeier, 2004; Rutstein *et al.*, 2007; but see Forstmeier (2007). It remains yet to be shown that such indexes of female mating preference are not influenced by personality. Finally, further studies should investigate the extent to which the influence of personality on mate-choice behavior translates into different mate-sampling tactics in the wild, and its possible effects on the selection pressures applying on males [14].

4.6. ACKNOWLEDGMENTS

We would like to thank Yannick Auclair, Tim Fawcett & Mark Gillingham for their comments on a previous draft, and Sébastien Motreuil for his assistance during bird care and devices building. This work was funded with a PhD grant provided to M.D. by the Conseil Régional de Bourgogne.

La première partie de cette thèse a été consacrée aux aspects méthodologiques inhérents à l'étude de la personnalité animale. Ainsi, nous avons démontré que certains traits de personnalité étaient inter-corrélés au sein d'un syndrome comportemental au niveau de notre population captive de Diamants mandarins, alors que d'autres, comme l'obstination (*obstinacy*), pouvaient représentés à eux-seuls une seule dimension de personnalité. Ces résultats suggèrent que l'évaluation de la personnalité chez les animaux, aussi intégrative que puisse paraitre la mise en évidence d'un syndrome comportemental, doit se garder de toute inférence abusive envers des dimensions de la personnalité n'ayant fait l'objet d'aucune analyse préalable.

Dans une seconde étude, nous avons montré que, à l'inverse de travaux récents ayant porté sur les mésanges charbonnières (*Parus major*), le taux de respiration engendré par le stress de la préhension par l'examinateur ne peut pas être utilisé comme un indicateur de la personnalité des Diamants mandarins. Cette découverte réduit ainsi l'espoir de mettre en place un test rapide, simple, non-invasif et possiblement valable au niveau inter-spécifique de la détermination de la personnalité des Diamants mandarins.

Enfin, lors de la troisième étude de cette première partie, nous avons mis en évidence les conséquences de la personnalité des femelles sur la mesure de différentes composantes du choix du partenaire dans un test de préférence par association spatiale. Ainsi, les femelles les plus exploratrices étaient moins sélectives, montraient des scores de préférence moins marqués mais plus répétables. Ces résultats indiquent que la personnalité des femelles utilisés dans des tests de préférence par association spatiale peut fortement biaiser l'interprétation des résultats en termes de pressions de sélection sexuelle et possiblement expliquer les résultats contradictoires publiés sur la même espèce dans différentes études de préférence sexuelle.

La seconde partie de la thèse s'attachera à étudier les liens entre stratégies d'approvisionnement et personnalité. Plus précisément, nous quantifierons les effets

conjoints de la personnalité et de la condition corporelle sur la motivation à s'alimenter. Dans une seconde étude, et suite à la mise en évidence de l'influence de la personnalité sur la compétition par interférence dans la première partie, nous évaluerons l'effet de la personnalité sur la compétition par exploitation au sein d'un jeu producteur-chapardeur.

ARTICLE IV

PERSONALITY AND BODY CONDITION HAVE ADDITIVE EFFECTS ON MOTIVATION TO FEED IN ZEBRA FINCHES *TAENIOPYGIA GUTTATA*

Morgan David, Yannick Auclair, Luc-Alain Giraldeau & Frank Cézilly

Ibis *in press*

5.1. ABSTRACT

Several hypotheses have been proposed to account for the adaptive evolution of personality, defined as inter-individual differences in behaviour which are consistent over time and across situations. For instance, the "pace-of-life syndrome" hypothesis suggests that personality evolved as a behavioural correlate to life-history trajectories varying within populations. Proactivity, corresponding to higher exploratory tendencies or higher boldness levels, has thus been linked to higher productivity or mortality rates. However, the extent to which proactivity is associated to a higher motivation to forage remains poorly explored. Moreover, although personality and its effects on foraging behaviour are usually considered to be independent of any motivational or nutritional state, few studies so far have challenged this. Here we show that personality traits, both individually or combined using a principal component analysis, and body condition have additive effects on latency to feed following food deprivation in the Zebra Finch, Taeniopygia guttata, with overall personality accounting for 41% and body condition for about 20% of the total variation in latency to feed. In accordance with the pace-of-life syndrome hypothesis, latency to feed was negatively related to the degree of proactivity, and positively related to body condition. Thus, proactive individuals, and birds in poorer condition, were quicker to start feeding after a deprivation period. The absence of a significant interaction between personality and body condition further suggests that the effect of personality was independent of body condition. We discuss the relevance of our results in relation to the different factors influencing foraging in birds. Moreover, we place our results within a life-history framework by emphasizing the correlated evolution of life-history traits and personality.

Keywords: exploration, feeding latency, life-history trade-offs, pace-of-life syndrome hypothesis, principal component analysis, productivity

5.2. INTRODUCTION

A growing literature shows the importance of the concept of personality, defined as inter-individual differences in behaviour that are consistent over time and across situations, in both captive and wild populations (Dingemanse et al. 2002, Montiglio et al. 2010, David et al. 2011a). These behavioural differences may evolve through both natural (Réale & Festa-Bianchet 2003) and sexual selection (Schuett et al. 2010). Several hypotheses, from the role of sexual selection (Schuett et al. 2010) to state-based differences (Dall et al. 2004), have been formulated to account for the evolution of personality within populations (Dingemanse & Wolf 2010). The "pace-of-life syndrome" hypothesis proposes that personality evolved as a behavioural correlate to life-history strategies varying at the population level (Réale et al. 2010). Thus, proactivity, corresponding to higher exploratory tendencies or higher boldness, associated with a high metabolic rate (Careau et al. 2010), high growth rates and a high productivity (Biro & Stamps 2008), may be constitutive of a fast pace-of-life (Réale et al. 2010). On the contrary, a slower pace-of-life may be related to reactive behaviours, such as shyness, a low metabolic rate, low growth rates and a low productivity (but see Adriaenssens & Johnsson 2009, 2011 and David et al. 2011b). Several studies have successfully linked high exploration tendencies or risk-prone behaviour to fitness-related traits such as survivorship (Biro et al. 2004), social dominance (David et al. 2011a) or food intake (Ward et al. 2004). To date, however, few studies have examined whether proactivity is associated to a higher motivation to engage in foraging activity (Hallerman et al. 2007). Yet, a higher motivation to feed is expected to help proactive individuals acquiring enough resources to sustain a high level of productivity.

Although personality and its effects on foraging behaviour are usually considered to be independent from inter-individual variation in motivational or nutritional state (Réale et al. 2007, Bergmüller 2010), this assumption has not been challenged experimentally. This is surprising given the recent idea that personality

and consistent inter-individual variation in metabolic rate may be subjected to correlated evolution (Careau et al. 2008, Biro & Stamps 2010). Indeed, it is intuitive to imagine that a consistently high or low resting metabolic rate is manifested, respectively, as higher or lower hunger levels, which in turn increases or decreases motivation to feed (Careau et al. 2008). Considering motivational and nutritional state is all the more so important that several tests designed to assess personality involve a foraging task, such as the measurement of neophobia or risk-taking (e.g. David et al. 2011a). Yet few studies so far have controlled for the influence of nutritional state on the expression of personality traits. More precisely, little is known on whether personality and natural variation in body condition have additive or interactive effects on individual motivation and foraging behaviour.

In the present study we investigate the joint effect of personality (David et al. 2011a), and body condition, on the motivation of captive Zebra Finches, Taeniopygia guttata, to feed after a period of food deprivation, assessed from the latency to forage. We expect birds with lower nutritional status (i.e. poorer condition) to be under higher risk of starvation and thus to show higher hunger levels and to be more willing to feed. Latency to start feeding is commonly used to measure individual motivation or willingness to feed in birds (e.g. Lazarus 1979, Sundberg 1995, Seferta et al. 2001) and may thus represent an adequate behavioural test from which to evaluate the joint influence of personality and natural variation in body condition on foraging behaviour.

5.3. METHODS

5.3.1. Study subjects

Forty-one wild-type young adult female Zebra Finches, previously used in another study (David et al. 2011a), constituted our study sample. Only females were used, as the present study was part of a larger research program on the influence of personality

on female sexual behaviour (David & Cézilly *in press*). Birds were kept in a single room and maintained in dyads in home cages (60 × 33 × 30 cm) for ten days before the experiments started. Temperature was maintained at 22 ± 2°C and the photoperiod was 13:11h light:dark (0730–2030 hours), with a 30-minute period of increasing light intensity in the morning and decreasing light intensity in the evening to imitate dawn and dusk. Each bird was identified by an orange numbered leg ring (AC Hughes, Hampton Hill, UK; size XF). Individuals were provisioned with millet seeds, cuttlebones and water ad libitum.

5.3.2. Assessment of personality traits

Four principal, inter-related, personality traits identified in Zebra Finches (David et al. 2011a) were assessed twice at a one-week interval at the rate of one trial per day for a given bird. Trials were performed in the same room in which the colony was maintained to prevent stress due to social isolation. Birds were food-deprived for 1h before each trial to standardize hunger levels (David et al. 2011a).

Activity - Intrinsic activity was recorded in a cage similar to home cages (a familiar environment) where birds were maintained. These cages contained four perches and two water dispensers. Birds were placed alone for 12 h in a home cage before the trial. We then recorded individual behaviour using a video-camera (JVC Everio GZ-MG20) which had been placed 50 cm in front of the cage 1h before the trial to avoid any novelty effect. We scored activity during consecutive periods of 5 s during a 10 min block. During each period, the bird was assigned a score of 1 if it moved between perches, or the equivalent distance on the floor. Birds had no access to any food source when tested.

Exploration tendencies – Exploration tests are sometimes referred to as novel environment tests (Dingemanse et al. 2002). Individual exploratory tendencies were

assessed in a large, unfamiliar cage (l×w×h: 140 × 140 × 70 cm) (David et al. 2011a) with opaque walls and a clear Plexiglas ceiling, containing five artificial trees (50 cm high) composed of four small branches each. A single bird was introduced into a small black box placed against one side of the apparatus. Experimenters then gently opened a trap from outside the room which enabled the individual to come inside the apparatus. Again, birds had no access to any food source when tested. The cumulative number of movements between trees and between branches recorded during 1 h was considered as the exploration score (David et al. 2011a).

Reaction to startle – Also known as "risk-taking behaviour" (van Oers et al. 2004c), this test aims at assessing individual latency to resume feeding after having been threatened off the feeder. Birds were placed alone for 12 h in a cage similar to a home cage before the trial. The trial consisted of replacing the feeder within the home cage after the one-hour food-deprivation period. A small device, corresponding to two washers wedged between the feeder top and the trap door above it, was set up and linked with a thin thread to the experimenter at the outside of the room. Pulling the thread caused the bird to fly off the feeder at the moment it came feeding. Then latency to resume feeding after this stressful event was considered as a measure of risk-taking behaviour (David et al. 2011a). Individuals resuming feeding early, i.e. more willing to take risks, thus had lower values.

Neophobia – A feeder was placed in one side of a cage similar to a home cage of an individual kept single for 12 h before the trial. In addition, an unfamiliar object (a small bag or a football figurine) was placed at 10 cm from the feeder. Neophobia was defined as the tendency to approach the feeder and consume seeds from it (David et al. 2011a). Thus, birds were food-deprived for one hour. Then, we replaced a feeder full of seeds in the cage, and added the unfamiliar object at 10cm from it. We then video-recorded birds' latency time to reach the feeder, the number of times it came feeding, the amount of time it fed, the latency time to perch near the feeder and the number of times it perched near the feeder. All these variables were reduced to a single synthetic value using a principal component analysis (David et al. 2011a) from

which we derived individual scores. Highest neophobia scores corresponded to individuals spending more time feeding near the novel object (i.e. less neophobic birds).

5.3.3. Motivation to feed

Motivation to feed was assessed from the latency to start feeding after a 1 h food-deprivation period. For the purpose of this test, birds were placed alone in a home cage the evening of the day before the trial. Seed feeders were removed from the home cage for 1 h while a miniature video-camera was placed 1 m in front of the cage in order for the birds to get used to it before the recording. After this period, a single feeder was gently replaced to its normal location at the furthest side of the cage. Individual behaviour was then observed from outside the room through the video-camera. Latency time to start feeding was then recorded to a maximum of 10 min. Individuals that did not came feeding during this period were assigned a score of 601 seconds. This test was performed in the middle of the session of behavioural trials, at the same day as the reaction to startle's test, and repeated twice at a one-week interval to check for consistency.

5.3.4. Morphometric measures

All morphometric measurements were recorded once on each of two days, one before and one after the behavioural trials. Tarsus length was measured with a digital calliper to the nearest 0.1 mm. Birds were weighed to the nearest 0.01 g with an electronic balance (OHAUS, Scout Pro SPU202) at the same time of day for each bird. The two values were averaged for each individual. We measured individual body condition as residuals of the linear regression of $\log_{10}$(average weight) on

$\log_{10}$(average tarsus length) (Carrascal et al. 1998, Strong & Sherry 2000, Schamber et al. 2009; see however Merilä et al. 2001).

5.3.5. Statistical analyses

Details on the consistency of personality traits can be found in David et al. (2011a). We here use the average of the two recorded values for each personality trait as our personality variables. As reaction to startle, neophobia, exploration tendencies and activity were previously found to be inter-related (David et al. 2011a), we computed a multivariate personality measure (hereafter termed the personality synthetic value) from a principal component analysis performed with these four traits. Principal component analysis' first axis explained 51.3% of variance. Eigenvectors of each personality trait on the axis were as follows: exploration tendencies: 0.46; activity: 0.53; neophobia: 0.52; reaction to startle: -0.50. Individuals defined by a high score were more active, more exploratory, less neophobic and more willing to take risks. They were therefore categorised as "proactive", whereas individuals with low scores were less active, less exploratory, more neophobic, less willing to take risks and categorised as "reactive" (Réale et al. 2007). Consistency of motivation to feed was assessed from the ANOVA's intra-class correlation coefficient (R) using Lessells and Boag's (1987) method. This procedure assesses the proportion of the total variance that is attributable to inter-individual variation versus intra-individual variation. Thus, the more the total variance is generated by differences between individuals, the more the behaviour is repeatable within individuals. Data for one of the two trials were missing for two individuals due to technical problems. These birds were thus assigned a single value. Therefore, the repeatability of "latency to start feeding" was estimated from 39 individuals. Mean latency to start feeding was otherwise calculated from the two trials and used thereafter. This latter variable was log-transformed to achieve

normality. For each of the two trials, the influence of the time when trials were carried out (morning or afternoon) on latency to start feeding was tested using t-tests.

We performed multiple linear regression analyses to assess the influence of each personality trait taken separately and its interaction with body condition on the latency to start feeding. Moreover, we computed the Pearson's correlation coefficient to provide an effect size of the relationship between the two variables. In addition, we ran a multiple regression analysis to evaluate and quantify the joint effect of global personality (as assessed from the personality synthetic value) and body condition on the latency to start feeding.

All analyses were conducted using JMP 5.0.1 statistical software (SAS Institute, Cary, NC).

5.4. RESULTS

Latency to start feeding did not differ between the first and the second trial (paired t-test: $t_{38} = -0.43$, $P = 0.67$), was highly consistent between trials ($R = 0.75$, $P < 0.0001$, $N = 39$), and did not depend on the time of the day when the trial was conducted (1st trial: t38.5 = 0.09, $P = 0.93$; 2nd trial: $t_{37} = 0.57$, $P = 0.57$). The median value of latency to start feeding, averaged across the two trials, was 45.5 sec (interquartile range: 14.1-154.5 sec.). All birds started feeding within the 10-minute time period.

Latency to start feeding was significantly influenced by neophobia (regression line's slope $b = -0.14$, $F_{1, 37} = 6.08$, $P = 0.02$; Pearson's $r = -0.34$), exploration tendencies ($b = -0.32$, $F_{1, 37} = 7.22$, $P = 0.01$; $r = -0.39$), reaction to startle ($b = 0.80$, $F_{1, 37} = 46.2$, $P < 0.0001$; $r = 0.76$) and activity ($b = -0.64$, $F_{1, 37} = 4.23$, $P = 0.05$; $r = -0.24$). There was no significant interaction between body condition and any personality trait affecting latency to feed ($P > 0.55$ for each model).

The multiple regression analysis revealed that both the personality synthetic value ($b = -0.26$, $R^2 = 0.41$, $F_{1, 37} = 25.0$, $P < 0.0001$; fig. 1a) and body condition ($b = 7.72$, R^2

= 0.19, $F_{1, 37} = 8.93$, P = 0.005; fig. 1b) affected latency to start feeding, but there was no significant interaction between the two predictor variables ($F_{1, 37} < 0.01$, P = 0.98),

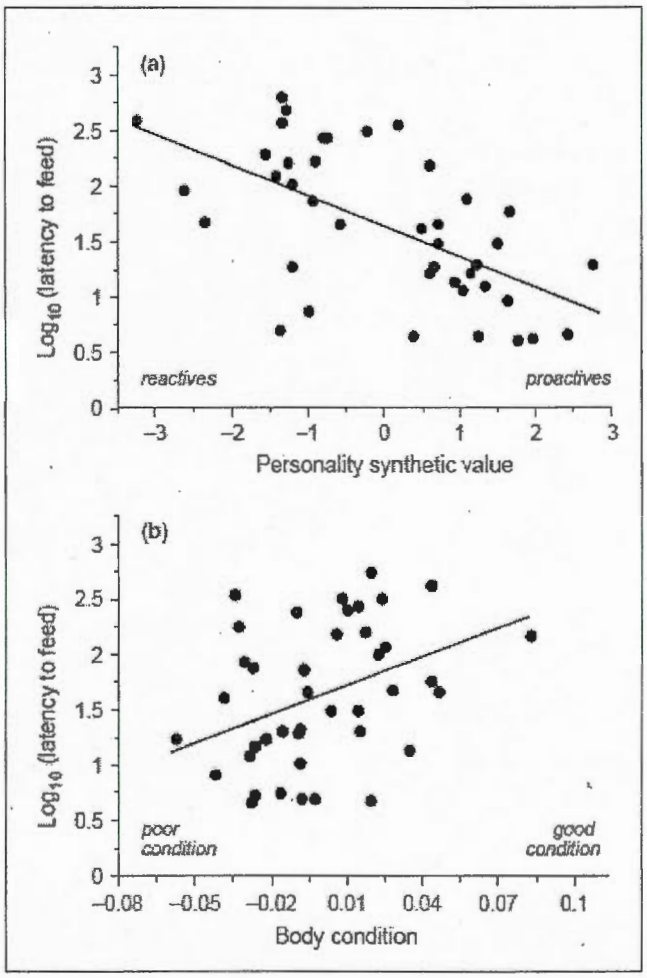

Figure 5.1. (a) Significant regression of latency to start feeding on the personality synthetic value of female Zebra finches. Proactive individuals started feeding sooner than reactive individuals. (b) Significant regression of latency to start feeding on body condition of female Zebra finches. Body condition was computed as the residuals of the linear regression of body mass on tarsus length. Individuals in poorer condition started feeding sooner.

indicating additive effects of body condition and personality. Thus, proactive individuals started feeding sooner than reactive ones after 1 h of food-deprivation. Similarly, individuals in poor condition started feeding sooner than individuals in good condition. The personality synthetic value was not related to body condition (Pearson's $r < -0.01$, $P = 0.99$, $N = 41$).

5.5. DISCUSSION

Our results show that birds in poorer body condition and those with more proactive behaviour (more active, exploratory, risk-taking and less neophobic) expressed a higher motivation to feed. Both neophobia and risk-taking were however assessed in a feeding context and may themselves reflect differences in feeding motivation mediated by nutritional state. However, we also found a positive link between exploration and activity, assessed in a non-feeding context, and feeding motivation. We are therefore confident that the link between proactivity and motivation to feed is biologically meaningful and not biased by individual nutritional state. Moreover, personality was not related to body condition. These findings add to the recent literature linking feeding behaviour to personality (Biro & Booth 2009), while emphasizing the role of personality on the outcome of behavioural tests. In guppies Poecilia reticulata for instance, unpredictable availability of food during early life lead individuals to adopt riskier behaviours (Chapman et al. 2010). In the present study, we found no significant interaction between body condition and personality on latency to start feeding, thus confirming one key-assumption of personality studies (Réale et al. 2007, but see Schuett & Dall 2009). Indeed, personality appears to be independent of body condition in female zebra finches, indicating that its influence on foraging behaviour is independent of hunger levels or state.

Various studies have used motivation to feed to assess, for example, food value, variance-sensitive foraging, or the decisions underlying individual behaviour

within the hiding/foraging trade-off (Martín et al. 2003). Our results indicate that, all else being equal, motivation to feed is independently affected by both personality and body condition. We therefore suggest that both should be taken into account when assessing inter-individual variation in feeding motivation, at least in Zebra Finches and possibly in other species. For example, it has been shown that Zebra Finches in poor condition had a higher feeding success in a scramble competition (David & Giraldeau 2012), perhaps simply because of their higher motivation to feed. However, a higher feeding success may not necessarily translate into an increase in condition or higher fitness as poor-condition zebra finches might have a higher basal metabolic rate (Mathot et al. 2009, Mathot & Giraldeau 2010). Personality and body condition may also affect the foraging decision rules used by individuals. For example, the devaluation of some food options may be confounded with a lower motivation to feed, possibly related to personality, and may affect the conclusions of prey-choice studies (Krebs et al. 1977). Further work may then benefit from considering variation in personality and body condition when investigating the foraging decision rules used by animals (David et al. 2011b).

Similarly, the possibility exists that the assessment of personality in a feeding context may be confounded by differences in body condition. Indeed, these trials commonly involve the measurement of individual willingness to feed near a novel object or the latency to forage. Intuitively, individual behaviour within such trials could be affected by nutritional state, just as body condition affected latency to start feeding in the present study. Thus we might predict that individuals in poorer condition would be bolder in feeding near a novel object or quicker to resume feeding after a perturbation. Conversely, personality trials excluding any foraging might be more reliable as they might exclude the possibility that willingness to forage drives behavioural performance. Despite this, we found that the expression of personality was not associated to body condition in the present sample. Yet, given the possible influence of condition of foraging behaviour, we feel that it is important to investigate the relationship between an index of nutritional state such as body condition, which

can be standardized using a food-deprivation period, and personality measures when trials involve a foraging task.

Finally, in accordance with the "pace-of-life syndrome" hypothesis (Careau et al. 2008, Réale et al. 2010), our results are consistent with the proposition by Biro and Stamps (2008) that inter-individual variation and within-individual consistency in personality may have co-evolved with differences in organisms' productivity (i.e. growth or fecundity), associated with differences in growth-mortality trade-offs within populations (Stamps 2007, Wolf et al. 2007). Several studies across taxa do show a positive relationship between proactivity and food intake or growth (Biro & Stamps 2008). In the present study, motivation to feed was highly consistent, as are personality traits assessed from the present sample (see David et al. 2011a). Moreover, feeding motivation and personality were correlated. Taken together, these findings suggest that different individuals may adopt different and consistent life-history trajectories. Higher motivation to feed might then be a behavioural mechanism favouring higher, and possibly opportunistic, food intake in proactive individuals, and as a consequence may positively affect growth rate and productivity in general (Hallerman et al. 2007, Millot et al. 2008).

5.6. ACKNOWLEDGMENTS

We thank Sébastien Motreuil for his assistance during bird care and devices building, Elise Melloul for her assistance during the experiments, Pete Biro, Wiebke Schuett, Simon Butler, Jeremy Wilson, and an anonymous referee for useful comments on a previous draft. This work was funded with both a PhD grant provided to M.D. and a master honorific grant to Y.A. from the Conseil Régional de Bourgogne. Experiments in this study were performed in accordance with the University of Burgundy's

procedures concerning animal ethics and British Ornithologists' Union statement of ethics.

ARTICLE V

PERSONALITY AFFECTS ZEBRA FINCH FEEDING SUCCESS IN A PRODUCER-SCROUNGER GAME

Morgan David, Frank Cézilly & Luc-Alain Giraldeau

Animal Behaviour 82, 61-67

6.1. ABSTRACT

Recent evidence strongly suggests that natural selection can favour the evolution of consistent individual differences in behaviour ('personalities'). Indeed, personality shows heritable variation and has been linked to fitness in many species. However, the fitness effects of personality are highly variable within and between species. Furthermore, the nature of the causal influence of personality on organism's fitness remains unclear so far. Competition has been proposed as a factor modulating this relationship. Thus, personality has been found to affect individual success in a competition by interference in a few species, but its influence in a scramble competition remains unexplored. Here we assessed exploratory tendencies (thought to be a key component of personality) in a model species, the zebra finch (*Taeniopygia guttata*). In a first session, we formed foraging flocks composed of four individuals with different exploration scores, and allowed them to repeatedly play producer-scrounger games. During a second session, individuals were reassigned to different flocks to check for consistency in the influence of exploratory tendency across different social contexts. Exploratory tendency influenced individual feeding success during the first session but not during the second one. High-exploratory birds were less successful at finding food (i.e. playing the producer tactic) and consequently had a lower feeding success, but were presumably able to adjust their behaviour between sessions. We discuss our results in relation to the interactive effects of both personality and experience, and highlight the role of competition processes on the evolution of personality.

Keywords: social foraging, behavioural syndrome, exploration, competition, speed-accuracy trade-offs, zebra finch, information use, scrounger tactic

6.2. INTRODUCTION

Consistent behavioural differences between individuals and across situations (so-called 'personalities') have recently become of prime interest to behavioural ecologists (Réale et al. 2007). Increasing evidence for animal personality raises the question of the factors at play in the maintenance of behavioural variation within populations (Sih et al. 2004a). To address this issue from an adaptive perspective, behavioural ecologists investigate the extent to which personality traits such as boldness, exploratory tendencies or risk-taking behaviour can evolve through natural selection (Quinn et al. 2009). Consistent behavioural variation has been described in a large range of species, from molluscs (Sinn et al. 2006), to arthropods (Johnson & Sih 2007) and vertebrates (David et al. 2011a). Personality traits also show substantial levels of additive genetic variation (Drent et al. 2003) and can have important consequences for fitness (Smith & Blumstein 2008). For instance, activity levels have been negatively related to survival in female red squirrels, *Tamiasciurus hudsonicus* (Boon et al. 2008).

The impact of personality on fitness has mainly been studied through its influence on reproductive success and survival (Smith & Blumstein 2008). However, the mechanisms responsible for these effects lack experimental attention and as a result remain largely unknown. In the great tit (*Parus major*) at least, exploratory tendencies predict differential survival across years and between sexes, and competition for food in the winter and for territories in the spring could explain these fluctuating pressures on personality (Dingemanse et al. 2004). Although foraging behaviour has already been related to fitness in several species (Ritchie 1990; Lemon 1991; Blanckenhorn 1991), direct evidence of an influence of personality on the outcome of foraging competition is rare (but see Fox et al. 2009; David et al. 2011a).

Foraging competition can be divided into two separate types. In interference competition, competitors physically interact to acquire specific food items. In scramble competition, they exploit the resource without physically interacting.

Individual success in both types of competition generally involves different abilities, such as dominance over conspecifics or a better capacity to detect cryptic food items. This explains why both types are traditionally investigated separately. Personality has been found to influence the likelihood of becoming dominant during interference competition for food in the mountain chickadee, *Poecile gambeli* (Fox et al. 2009), in the zebra finch, *Taeniopygia guttata* (David et al. 2011a), and in the three-spined stickleback, *Gasterosteus aculeatus* (Ward et al. 2004). To date, however, few studies have examined the effect of personality on the outcome of scramble competition (Beauchamp 2001). For instance, shy barnacle geese preferentially use social information when feeding in groups (Kurvers et al. 2010) and therefore are more likely to exploit the discoveries of group mates. As the two types of foraging competition involve different abilities, individuals that are successful in interference competition may not necessarily be successful in scramble competition. This could lead both types of competition to exert contrasting selection pressures on the evolution of personality.

In the present study, we address this issue by investigating the behaviour of individuals varying in personality types while engaged in a producer-scrounger foraging game (Barnard & Sibly 1981; Giraldeau & Caraco 2000). In this system, individuals forage in a group and allocate their sampling effort between searching their own food (the producer tactic) and exploiting flock mates' discoveries (the scrounger tactic). This foraging game enables us to investigate the influence of personality on the use of both personal and social information associated with alternative foraging tactics, and the resulting payoffs leading to fitness consequences in scramble competition. We first formed foraging flocks composed of individuals with different exploratory tendencies. Then we recorded their feeding success and their use of both producer and scrounger foraging tactics across repeated trials. Birds were tested in two different flocks with different flock mates to assess both the consistency of exploration tendency on foraging behaviours and its flexibility (Briffa et al. 2008; Dingemanse et al. 2010). We chose the zebra finch as our model

organism as it has already been successfully used within studies of personality (Schuett & Dall 2009; David et al. 2011a) and social foraging (Beauchamp 2006).

6.3. METHODS

6.3.1. Study subjects

Zebra finches are small Australian passerine birds living and feeding in large colonies, from ten to hundreds of individuals, in the wild (Zann 1996). Feeding flocks are formed either by individuals joining others already feeding on the ground or by individuals landing on the ground in a cohesive flock (Zann 1996). These feeding habits indicate that zebra finches can rely on flock mate's behaviour to locate food patches and thus attempt to scrounge from their discoveries. Fifteen male and 15 female zebra finches, all between two and three months old, were purchased from a local supplier (L'oisellerie de l'Estrie, Québec). Before the experiments, birds were kept in three adjacent rooms in same-sex groups of two to three individuals in small home cages (29 × 52 × 38 cm) containing four feeders and four perches. Room temperature was maintained at 24±1 °C on a 12:12 light cycle (0800-2000 hours EDST). Millet seeds, water and cuttlebones were provided ad libitum while vegetables and an egg mixture were occasionally offered. Each individual wore a numbered orange plastic leg ring (AC Hughes, Hampton Hill, UK; size XF) allowing individual identification. After the experiment, birds were kept in groups of two to be used in subsequent studies.

6.3.2. Assessment of exploratory tendencies

Following previous studies of birds' exploratory behaviour (Dingemanse et al. 2002; David et al. 2011a), individual exploratory tendencies were assessed twice with a 1-week interval in a large cage (the exploration apparatus, 120 × 120 × 60 cm) with

which the birds were unfamiliar (Réale et al. 2007). This cage had opaque walls, a wire mesh ceiling and comprised five artificial trees each with four small branches. Birds were deprived of food for 1 h to control for feeding motivation before being introduced singly in a black box placed against a small sliding door on one side of the apparatus. Experimenters then gently opened the door with a pulley system from outside the room, which successfully motivated birds to enter the apparatus. Individual behaviour inside the apparatus was recorded for 1 h, using a video camera (Sony HDR XR500) placed 1 m above it. During the analysis, the experimenter (MD) recorded the number of movements between trees and between each branch of a single tree. Each movement was easily identifiable through a short flight between two perches. Birds did not perform any other jumps or lateral movements on the same perch. Following this experiment, individuals were sorted into four categories as a function of the cumulative number of movements they performed within the apparatus, averaged across the two trials. Zebra finches generally show a highly consistent behaviour in the apparatus during 30- or 60-minute trials (M. David, unpublished data), suggesting that individual behaviour during exploration trials is not the mere result of reaction to stress or attempts to escape and reliably represent an intrinsic tendency to move around in an unfamiliar environment. Birds in the upper-third, middle-third and lower-third of the distribution were respectively considered as high-, medium- and low-exploratory individuals, irrespectively of gender. As six out of the tested birds (three males and three females) did not come out of the small black box, they constituted a fourth category (NA) of individuals which had no quantitative exploratory score but were still used in the subsequent parts of the experiment:

6.3.3. Producer-scrounger game

Foraging experiments started one week after the last exploration trial. Each flock was composed of one randomly chosen individual from each of the four exploration

categories. We did not associate birds that had previously been housed together, to avoid any potential effect of familiarity. We also decided to separate the males and females into same-sex foraging flocks to avoid any interference from intra-sexual competition or male courtship.

Foraging experiments were divided into two similar sessions lasting 3 days each (Sessions A and B). On the first day of a session, individuals were given a unique combination of blue and light blue leg rings for identification from the video footage. Thus, in addition to their orange identification leg ring, the four birds in each flock wore one of the following colour combinations: light blue-light blue, light blue-blue, blue-light blue, blue-blue. We chose this colour as it has no effect on sexual or agonistic inter-individual interactions (Burley et al. 1982; David et al. 2011a). Ring-colour combination had no effect on any recorded variables ($P > 0.10$ for all tests). Each bird was then placed with its flock mates inside a large aviary (1.5 × 3.8 × 2.3 m) containing two tables (1.4 × 0.7 m), which supported a foraging grid with 64 small wells (1.6 in diameter and 1 cm deep) every 8.1 cm. Two large perches and two water containers were placed on one table. The aviaries were on the same light cycle and the same temperature as the rooms in which the birds were previously held. To help familiarize the birds with the aviary and the foraging grid, each well was filled with millet seeds on the first day.

On the second day, the grid and the aviary floor were cleaned in the morning to prevent birds from feeding on seeds left on the floor. Birds were then deprived of food for 1 h before training experiments. Then, each flock was given five white millet seeds per well in 10 wells every hour for 7 h, enabling them to forage in flocks during seven training trials. Wells to be filled were randomly chosen for each trial. Each flock was given seeds ad libitum in all grid wells for the rest of the second day. The same procedure was performed again on the third day (testing phase) except that each flock underwent five experimental trials that were video-recorded and used for analysis. Afterwards, individuals were returned to their home cages in groups of two to three individuals per cage and given seeds and water ad libitum.

Birds were allowed to rest for 4 days before undergoing the same procedures but with different flock mates.

6.3.4. Note on sample sizes

We tested six flocks (three per sex) of four birds per session. Twenty-four birds were thus used during session A. We re-used 18 of these birds during session B to test behavioural consistency across flocks. Because of our experimental design (4 different birds in 3 same-sex flocks), it was impossible to form three same-sex flocks in session B which composition entirely differed from session A. That is why we re-used only 18 birds and introduced six new birds (three males and three females, four coming from the low-exploration category, one from the medium and one from the high exploration category) in session B. In session B, birds were also randomly associated to flock mates with which they had never interacted before. However, due to a lack of available individuals, two birds were tested together in the same flock in both sessions. Removing these individuals from the analyses does not substantially change the results.

To sum up, within-session tests were performed on 24 individuals (six flocks of four individuals) whereas between-sessions tests were performed on 18 birds.

6.3.5. Data analysis

During video analysis, we recorded the arrival rank on the grid so that the bird landing first obtained the score 1. The last bird to land obtained the score 4. We recorded the individual number of producing events, corresponding to a bird finding a hitherto undiscovered well containing seeds, and the number of seeds eaten ('produced'). We recorded the individual number of scrounging events, corresponding to a bird joining a well on which other birds were already feeding or had just left within a few seconds, and the number of seeds they scrounged. The variable "number of seeds ingested" corresponded to the sum of both the number of

seeds produced and scrounged over the five trials. "Finder's share" was defined as the number of seeds eaten per producing events. As one bird ingested no seeds during session A, analyses involving the variable "proportion of seeds scrounged" was performed with only 23 individuals.

Behavioural consistency was assessed between the two trials for exploration tendencies and between the five trials of a given session for foraging behaviours, by calculating the intra-class correlation coefficient (repeatability, R), using the method of Lessells & Boag (1987). A 95% confidence interval was also calculated for each coefficient (Nakagawa & Schielzeth 2010). As two individuals from the low-exploration category did not come out of the black box during one exploration trial, repeatability was calculated from only 22 individuals (the six individuals from the NA category were discarded from this analysis). Exploration tendency values were averaged from the two trials and foraging behavioural values were averaged from the five trials of a given session for each variable and used thereafter.

The number of individual foraging events (occurrence of producing and scrounging) was always strongly correlated with the number of seeds eaten using each tactic within each session (Pearson correlations: session A: "producing events" vs. "seeds produced": $r_{23} = 0.89$; "scrounging events" vs. "seeds scrounged": $r_{23} = 0.96$; "proportion of scrounging events" vs. "proportion of seeds scrounged": $r_{22} = 0.95$; session B: "producing events" vs. "seeds produced": $r_{23} = 0.92$; "scrounging events" vs. "seeds scrounged": $r_{23} = 0.96$; "proportion of scrounging events" vs. "proportion of seeds scrounged": $r_{23} = 0.97$; $P < 0.0001$ for all tests). For conciseness we only report the analyses performed on the variables "number of seeds produced", "number of seeds scrounged" and "number of seeds ingested". Analyses conducted with the variables "number of events" yielded the same results.

The influence of exploratory tendency on foraging behaviour was tested using non-parametric Friedman tests. This enabled us to control for the non-independence of data within flocks, i.e. to control for the possibility that the behaviour of a focal individual is influenced by flock mates. Paired t-tests were used to check if an

individual's foraging behaviour differed significantly between the two sessions. The influence of exploratory tendency on between-session variation in individual foraging behaviour was tested using non-parametric Kruskal-Wallis tests. Only two birds from the low-exploration category were tested during both sessions (see *Note on sample sizes* subsection). We then excluded this category from the analyses based on between-session variation in behaviour to avoid any sample size effect, and only used the three other exploration categories (NA, medium and high).

The relationship between arrival rank on the grid and foraging behaviour was tested using Pearson correlations.

Variables were log or root transformed to reach normality when needed. Statistical analyses were performed with JMP 5.0.1 and Statview 5.0 software.

6.4. RESULTS

6.4.1. Exploratory tendencies' consistency

The number of movements performed within the exploration apparatus was highly consistent between the two trials (R = 0.60, 95% CI: 0.36-0.84, $F_{21,43}$ = 4.05, P = 0.001, N = 22; Fig. 6.1.) and did not differ between the sexes (t_{22} = -0.46, P = 0.651).

6.4.2. Foraging behaviour consistency within and between sessions

Mean number of seeds produced per trial was 8.9 ± 2.6 (mean ± 95% CI) in session A and 8.7 ± 1.8 in session B. Mean number of seeds scrounged per trial was 2.1 ± 0.9 in session A and 2.4 ± 1.1 in session B. Mean finder's share was 2.2 ± 0.3 seeds in session A and 2.8 ± 0.2 seeds in session B. Arrival rank, number of seeds produced, scrounged, ingested, and finder's share were significantly repeatable across trials in females within each session (Table 6.1.). In males, the size of the finder's share was not repeatable while arrival rank and proportion of seeds scrounged were not

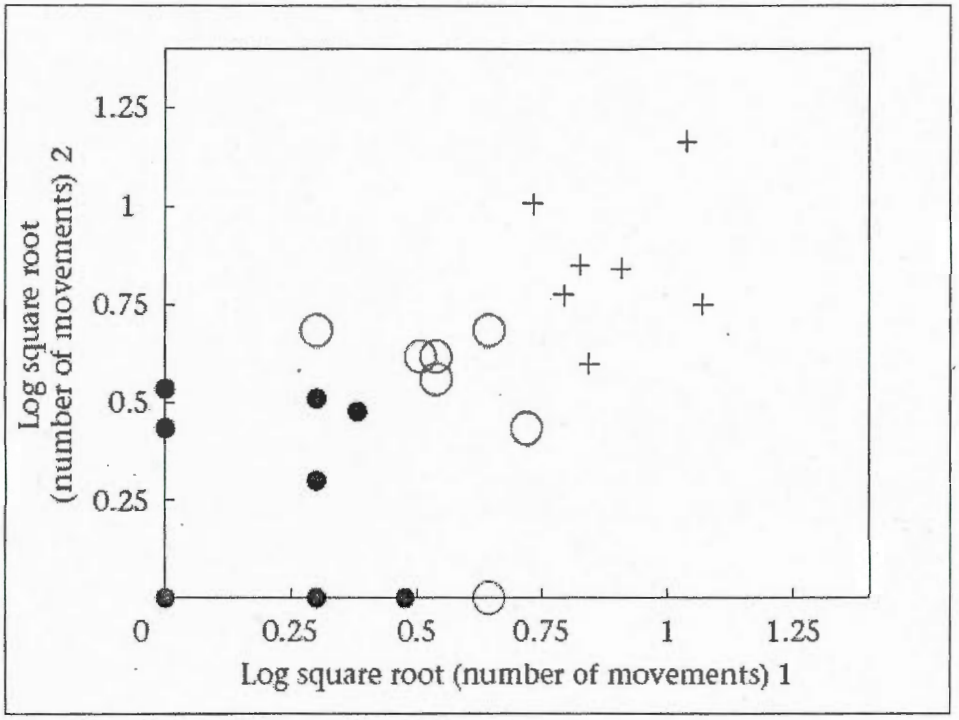

Figure 6.1. Relationship between the two individual exploration scores measured as the number of movements performed within the exploration apparatus. Birds were thereafter separated into four exploration categories: a high-exploratory category (+), a medium-exploratory category (○) and a low-exploratory one (●). The fourth category (NA) corresponded to the birds which never entered the exploration apparatus and stayed in the small black box.

	Session A				Session B			
	Males		Females		Males		Females	
Measured variable	*R* (CI)	*P*	*R* (CI)	*P*	*R* (CI)	*P*	*R* (CI)	*P*
Arrival rank on the grid	0.07 (−0.18–0.32)	0.21	0.67 (0.42–0.92)	<0.001	0.53 (0.23–0.84)	<0.001	0.39 (0.06–0.71)	<0.001
Number of seeds produced	0.51 (0.19–0.82)	<0.001	0.65 (0.39–0.91)	<0.001	0.37 (0.04–0.70)	<0.001	0.58 (0.29–0.87)	<0.001
Number of seeds scrounged	0.49 (0.17–0.81)	<0.001	0.59 (0.30–0.87)	<0.001	0.45 (0.12–0.77)	<0.001	0.71 (0.48–0.94)	<0.001
Proportion of seeds scrounged	0.16 (−0.17–0.49)	<0.001	0.68 (0.43–0.93)	<0.001	0.33 (0.05–0.75)	<0.01	0.56 (0.26–0.86)	<0.001
Number of seeds ingested	0.60 (0.31–0.89)	<0.001	0.64 (0.37–0.91)	<0.001	0.28 (−0.04–0.59)	<0.01	0.56 (0.26–0.85)	<0.001
Finder's share	0.10 (−0.23–0.54)	<0.001	0.48 (0.15–0.80)	<0.001	0.09 (−0.18–0.35)	0.18	0.17 (−0.13–0.46)	0.05

Values in parentheses correspond to the coefficient's 95% confidence interval (CI).

Table 6.1. Within-session repeatability estimates and associated significance of the variables recorded during producer-scrounger trials

repeatable only during session A (Table 6.1.). Males and females significantly differed in arrival rank consistency in session A, as neither confidence intervals overlap. No other repeatability estimate significantly differed between sexes. Between sessions, no variable was found to be significantly repeatable, except female arrival rank (Table 6.2.).

6.4.3. Effects of exploratory tendencies on foraging tactic use

Arrival rank on the grid was not affected by exploratory tendency (session A: χ^2 = 1.40, df = 3, P = 0.71; session B: χ^2 = 0.75, df = 3, P = 0.86). In both session A and B, exploratory tendencies were not linked to the number of seeds scrounged (session A: χ^2 = 2.53, df = 3, P = 0.47; session B: χ^2 = 1.60, df = 3, P = 0.66) nor the proportion of seeds scrounged (session A: χ^2 = 0.36, df = 3, P = 0.95; session B: χ^2 = 2.00, df = 3, P = 0.57). However, the number of seeds produced (χ^2 = 9.00, df = 3, P = 0.03), the total number of seeds ingested (χ^2 = 9.60, df = 3, P = 0.02), and to some extent the finder's share (χ^2 = 7.32, df = 3, P = 0.06), were all associated with exploration

	Males		Females	
Measured variable	*R* (CI)	*P*	*R* (CI)	*P*
Arrival rank on the grid	0.28 (−0.45–1.01)	0.21	0.61 (0.12–1.11)	0.02
Number of seeds produced	−0.05 (−0.84–0.74)	0.55	0.22 (−0.53–0.98)	0.26
Number of seeds scrounged	0.48 (−0.14–1.09)	0.07	0.36 (−0.33–1.05)	0.14
Proportion of seeds scrounged	0.47 (−0.14–1.09)	0.07	0.37 (−0.31–1.05)	0.13
Number of seeds ingested	0.16 (−0.61–0.94)	0.32	0.36 (−0.34–1.05)	0.14
Finder's share	−0.14 (−0.92–0.64)	0.65	−0.21 (−0.97–0.54)	0.72

Values in parentheses correspond to the coefficient's 95% confidence interval (CI).

Table 6.2. Between-session repeatability estimates and associated significance of the variables recorded during producer-scrounger trials

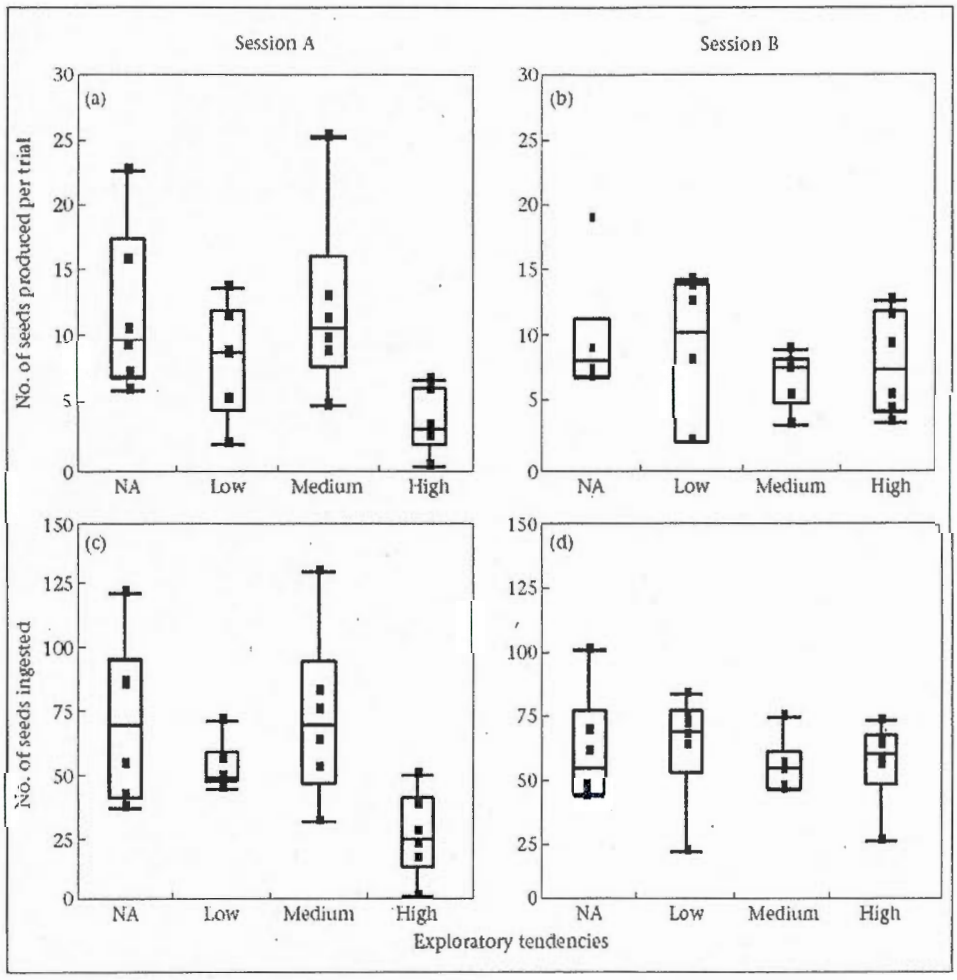

Figure 6.2. Influence of exploratory tendencies (NA, low, medium and high) on the mean number of seeds produced per trial (*a*) and the total number of seeds ingested in session A (*c*) and in session B (*b* & *d*). The effects of exploratory tendency on feeding success are significant in session A but not in session B. Boxes show the 75th and 25th percentile and the median in between. Whiskers are computed as the 75th /25th percentile +/- 1.5 × the interquartile range.

tendencies in session A (Fig. 6.2.a,c), but surprisingly not in session B (seeds produced: $\chi^2 = 1.17$, $df = 3$, $P = 0.76$; seeds ingested: $\chi^2 = 2.60$, $df = 3$, $P = 0.46$;

finder's share: $\chi^2 = 6.20$, $df = 3$, $P = 0.10$; Fig. 6.2.b,d). Specifically, high-exploratory individuals had a lower feeding success, produced less and had a lower finder's share than individuals from the other exploration categories in session A. The total number of seeds ingested by all individuals did not significantly differ between the two sessions ($t_{17} = -0.56$, $P = 0.58$).

The analyses linking feeding success, variation in foraging tactic use between sessions and exploratory tendency are summarized in table 6.3. High-exploratory individuals showed a significant increase in the total number of seeds ingested between session A and B (Fig. 6.3.a, Table 6.3.). This increase was due to a higher number of seeds produced (Fig. 6.3.b, Table 6.3.) and a higher finder's share in session B compared to session A (Table 6.3.). The number of seeds scrounged and the proportion of seeds scrounged did not increase between both sessions. Both medium-exploratory individuals and birds from the NA category showed a significant decrease in the total number of seeds ingested between sessions A and B. This decrease was

	NA		Medium		High	
Measured variable	%	t, P	%	t, P	%	t, P
Number of seeds produced	+5.0	16.71 <0.001	−27.7	14.64 <0.001	+118.2	6.81 0.002
Number of seeds scrounged	−51.0	−2.34 0.07	−38.0	−2.33 0.08	+18.0	−4.81 0.02
Proportion of seeds scrounged	−58.3	−2.24 0.08	−20.0	−2.8 0.05	−18.1	−5.17 0.01
Number of seeds ingested	−7.7	−11.45 <0.001	−28.8	−8.97 0.001	+47.2	−6.94 0.002
Finder's share	+12.0	−1.26 0.26	+3.5	−0.59 0.59	+58.2	−2.95 0.04

Statistical tests correspond to the significance of the difference between sessions A and B.

Table 6.3. Between-session variation in foraging behaviours recorded during producer-scrounger trials as a function of exploration categories

due to a lower number of seeds produced in session B compared to session A. As for high-exploratory birds, the number of seeds scrounged and the proportion of seeds scrounged did not vary between sessions. Therefore, between-session variation in the number of seeds ingested (H = 9.63, df = 2, P = 0.01) and the number of seeds produced (H = 7.89, df = 2, P = 0.02) differed between exploration categories. However, neither the variation in the number of seeds scrounged (H = 1.54, df = 2, P = 0.46), the proportion of seeds scrounged (H = 1.22, df = 2, P = 0.54), nor the finder's share (H = 4.13, df = 2, P = 0.13) did.

Finally, foraging tactic use was related to arrival rank on the grid both in session A (number of seeds produced: r_{23} = -0.44, P = 0.03; number of seeds

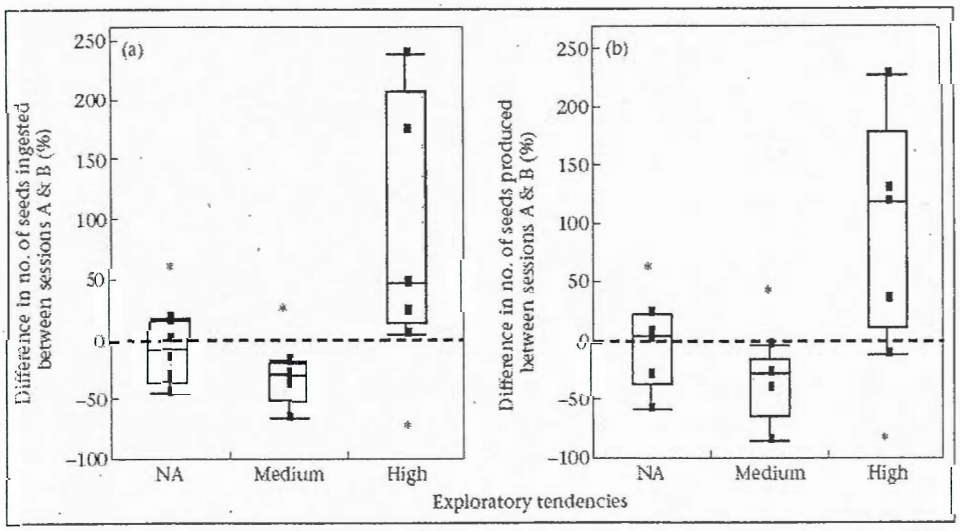

Figure 6.3. Influence of exploratory tendencies (NA, medium and high) on the difference in the individual number of seeds ingested (*a*) and produced (*b*) in the two different flocks between sessions. The difference is significantly different from zero for each exploration category, and the influence of exploratory tendency on these differences is also significant. Asterisks indicate that the between-session change differs significantly from zero. Boxes show by the 75th and 25th percentile and the median in between. Whiskers are computed as the 75th /25th percentile +/- 1.5 × the interquartile range.

scrounged: $r_{23} = 0.35$, $P = 0.10$; proportion of seeds scrounged: $r_{22} = 0.49$, $P = 0.02$) and in session B (number of seeds produced: $r_{23} = -0.56$, $P = 0.01$, Fig. 6.4.a; number of seeds scrounged: $r_{23} = 0.34$, $P = 0.10$, Fig 6.4.b; proportion of seeds scrounged: $r_{23} = 0.51$, $P = 0.01$, Fig. 6.4.c). Moreover, feeding success was marginally related to arrival rank in session A ($r_{23} = -0.38$, $P = 0.07$) and significantly related in session B ($r_{23} = -0.46$, $P = 0.03$; Fig. 6.4.d). Birds that were the first to land on the grid

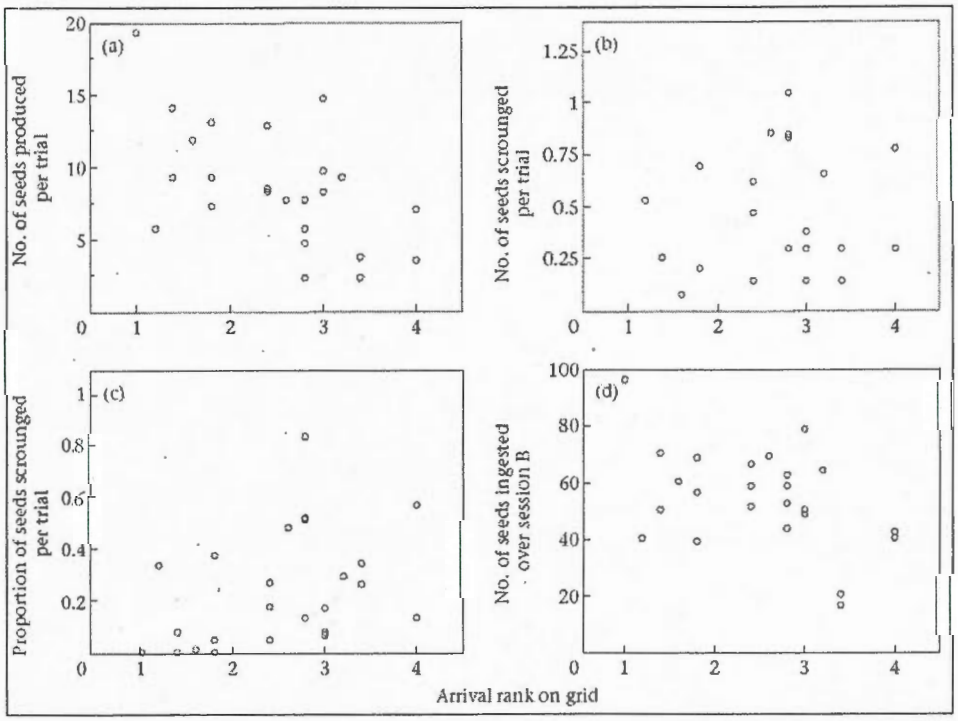

Figure 6.4. Correlation between arrival rank on the grid in session B and *a*) the mean number of seeds produced per trial in session B, *b*) the mean number of seeds scrounged per trial in session B, *c*) the mean proportion of seeds scrounged per trial in session B and *d*) the total number of seeds ingested over the session B. Birds which are the first to land on the grid are more likely to produce and have a higher feeding success, whereas birds which are the last to land are more likely to scrounge and have a lower feeding success. Mean proportion of seeds scrounged was log-transformed to reach normality.

6.5. DISCUSSION

Our results reveal that both exploration tendencies and foraging behaviours were repeatable within sessions, suggesting that zebra finches show consistent inter-individual differences when foraging within flocks. Only the repeatability of arrival rank during the first session differed between sexes and the magnitude of the finder's share was repeatable only in females during the first session. This lack of consistency suggests that individual zebra finches do not differ in their ability to secure a food patch they have just discovered, thus minimizing the role of interference competition, dominance and aggressiveness during scramble competition. This finding can be contrasted with a recent work by David et al. (2011a) who reported that individual personality influences social dominance and preferential access to a single feeder in the same species. The discrepancy between the latter and the present study mainly lies in food availability which was here greater (five seeds in ten wells) than in David et al.'s (2011a) study (a single feeder in a six-individual group) (see Dubois & Giraldeau 2004 for a study on a related topic). This could explain why interference competition seems to be minimal in the present study. Yet, even if aggressive interactions were nonexistent during trials, we cannot totally discard the possibility that dominant birds may intimidate their flock mates.

Although our experiments were performed on a small number of individuals, they were designed specifically to sort flock mates into different exploration tendency categories and so maximise within-flock variation in behaviour. Moreover, individuals were highly consistent in their behaviour within the same flock, reducing the likelihood of committing type I errors and confirming that observed variation was not the mere effect of random decisions. Although we only focused on exploratory behaviour, we are confident that our results can be generalized to global personality, as David et al (2011a) recently demonstrated that exploratory tendency was part of a wide behavioural syndrome including neophobia, risk-taking behaviour and activity in zebra finches.

We found that personality influences the number of seeds that individuals ingest during a scramble competition. Here high-exploratory individuals had a lower feeding success. Yet, this effect was found only during the first testing session. High-exploratory birds adjusted their behaviour during the second session, and thus reached a similar success as individuals from the other exploration categories. A possible explanation for the observed change between sessions and the consequent lack of behavioural consistency could be that the influence of personality on individual behaviour is greater when individuals face a novel situation containing in our case both new conspecifics and unfamiliar foraging payoffs. When this happens, birds would rather be influenced by an intrinsic tendency, such as personality, because of a lack of experience, than trying to learn to adjust to the unfamiliar situation. Further experiments need to be designed to test the hypothesis that both personality and experience have interactive effects on foraging behaviour.

The lower patch production rate of high-exploratory individuals suggests that food searching efficiency in zebra finches could be related to personality. For instance, Beauchamp (2006) showed in zebra finches that different individuals had different feeding efficiencies, measured as the number of seeds an individual can find on a grid in a given time period. Moreover, less efficient birds scrounged more in subsequent producer-scrounger games. Future studies should explore the possibility that variation in personality could be related to a so-called 'speed-accuracy trade-off' (Chittka et al. 2009), linked to foraging efficiency. In foraging zebra finches, we would expect high-exploratory individuals to be faster at sampling the grid while being less accurate in detecting seeds. In contrast, less exploratory birds should be slower at sampling wells but less likely to miss the full ones.

We did not find any effect of personality on the propensity to use social information when foraging (i.e. scrounging). This result can be contrasted with those of two related studies: a study of the barnacle goose, *Branta leucopsis* (Kurvers et al. 2010) and another on zebra finches (Beauchamp 2006). Our result differ from those obtained with the barnacle goose in which "reactive" individuals (less exploratory

individuals in the present study) scrounged more than "proactive" ones (Kurvers et al. 2010). This difference may be associated with the link between personality and landing order between the two species. Indeed, in foraging barnacle geese, proactive individuals are more likely found to lead the group, while reactive individuals are more likely to follow (Kurvers et al. 2009). Proactive individuals are more likely therefore to be the first to arrive on food patches while reactive ones join other's discoveries and scrounge. In zebra finches, the link between scrounger tactic use and arrival rank on food patch was documented by Beauchamp (2006) and the present study, but unlike for the barnacle goose, we found no link between exploratory tendency and arrival rank on the grid (but see Beauchamp 2000).

A recent study conducted on zebra finches found that high-exploratory individuals were dominant and had a preferential access to a single feeder in interference competition (David et al. 2011a). These results are in contrast to those we obtained here. Taken together, they suggest that individuals of the same personality type may be variably successful in different competitive contexts, and thus face different selection pressures in different competitive situations. High-exploratory individuals may be more successful in interference competition but less successful in scramble competition. These differential effects of competition could play a role in the maintenance of personality variation within populations. Following this reasoning, the extent to which individuals of a given species are subject to each type of competition during their lives can influence the type of personality that will be ultimately selected in competitive contexts.

6.6. ACKWNOLEDGMENTS

We thank Sasha Dall and Denis Réale for useful discussions on this paper, Tim Fawcett for valuable comments on a previous draft and two anonymous referees who helped improve the manuscript. This study and MD were financially supported by

funds from an NSERC Discovery Grant to L-AG. MD received additional financial support from a Frontenac Scholarship from FQRNT. All procedures applied to animals in this study complied with guidelines from the Canadian Council for Animal Care and were approved under protocol 0210-676-0211 of the UQAM committee for animal care.

Dans la seconde partie de cette thèse nous avons exploré les relations entre la personnalité et les comportements d'approvisionnement. Dans une première étude nous avons montré que la motivation à s'alimenter dépendait à la fois de la personnalité des individus et de leur condition corporelle, agissant de manière indépendante. Ces résultats vont dans le sens de l'hypothèse du rythme de vie proposant que la personnalité des animaux est associée de manière adaptive à leur trajectoire d'histoire de vie et leur productivité.

Dans une deuxième étude, nous avons montré que, à l'inverse des résultats obtenus en situation de compétition par interférence, les Diamants mandarins proactifs souffraient d'un succès d'approvisionnement inférieur à celui des individus réactifs en situation de compétition par exploitation, ici un jeu producteur-chapardeur. Nous avons suggéré que les variations de personnalité pouvaient être maintenues au sein des populations de Diamants mandarins par leurs effets différentiels sur le succès d'approvisionnement en fonction du type de compétition.

L'étude de la personnalité se caractérise par la constance de son influence sur les comportements à travers les contextes. Toutefois, à l'instar des comportements d'approvisionnement, les effets de la personnalité sur les comportements sexuels ont plutôt été négligés jusqu'à maintenant. Ainsi, dans cette dernière partie, nous étudierons l'influence de la personnalité sur le choix du partenaire lorsque de l'information sociale est disponible en plus de l'information acquise de manière personnelle. Enfin, nous produirons une synthèse des études ayant jusqu'à maintenant lié personnalité et sélection sexuelle en insistant sur les implications et les enjeux d'une telle approche à la fois pour l'étude de la personnalité animale et de la sélection sexuelle.

ARTICLE VI

THE EFFECTS OF PERSONALITY AND DEMONSTRATOR'S CONDITION ON MATE-CHOICE COPYING IN ZEBRA FINCHES (*TAENIOPYGIA GUTTATA*)

Morgan David, Yannick Auclair & Frank Cézilly

7.1. ABSTRACT

Increasing evidence shows that a vast array of organisms within different mating systems can trade personal versus social information when choosing a mate. However, empirical evidence suggests that variation exists in the differential use of these two types of information in a mating context. The influence of both intrinsic and extrinsic factors on social information use in a mating context, i.e. mate-choice copying, has been neglected hitherto. Here we investigate to what extent both personality and demonstrator's body condition can affect mate-choice copying in the zebra finch (*Taeniopygia guttata*). First we assessed different facets of focal female's personality and body condition, computed as residual body mass. Then we evaluated females' tendency to increase their preference for an initially non-preferred male after watching him paired to another female. We provide evidence for substantial variation in how much females rely on conspecifics' presence after a six-day period of observation. Overall yet, the evolution of preference for the least-preferred males did not differ from a null evolution. In addition, the evolution of preference was similar to the evolution quantified in a control group where only male pairs could be observed. Using an information-theoretic approach, we found no effect of focal female's personality or body condition on mate-copying tendency, whereas the evolution of preference for the initially least preferred male was negatively related to the condition of demonstrator females. Focal females thus may rely more on poor-condition conspecifics when using social information in a mating context. We discuss our results in relation to the relevance of mate-choice copying in animals and to the role and characteristics of demonstrators.

Keywords: decision rules – information-theoretic approach – social information use – spatial association tests – repeatability

7.2. INTRODUCTION

When choosing a mate, females can rely on either personal or social information or both (Brooks 1998; Kendal et al. 2009). On the one hand, pairing decisions depend on a suite of cognitive mechanisms involving the assessment of males' characteristics and the comparison to an innate or learned sexual preference (Bateson and Healy 2005). On the other, female decisions can be influenced by the observation of conspecifics mating with a given male, so-called "mate-choice copying" (Godin et al. 2005; Galef et al. 2008). The relevance of the use of social information in a mating context lies in the increase in the variance of male mating success at the population level (Wade and Pruett-Jones 1990), with the culturally-transmitted sexual preferences mediating the strength and direction of the sexual selection pressures acting on male traits (Alonzo 2008).

Although mate-choice copying has primarily been thought to be restricted to a small number of lekking or promiscuous organisms (Vakirtzis and Roberts 2010), recent evidence demonstrates that it can actually occur in numerous species, from fruit flies, *Drosophila melanogaster* (Mery et al. 2009) to sailfin mollies, *Poecilia latipinna* (Hill and Ryan 2006). Moreover, species within which both sexes heavily invest in reproduction, such as monogamous organisms, may also use social cues when choosing a mate (Swaddle et al. 2005; Frommen et al. 2009).

Despite this growing body of evidence, studies still commonly show large variation in female propensity to copy each other mate-choice (Vukomanovic and Rodd 2007). In zebra finches (*Taeniopygia guttata*) for instance, different studies have exhibited contrasted results regarding the importance of mate-choice copying at the population level (Doucet et al. 2004; Swaddle et al. 2005). Observed between-individual variation in mate-copying tendencies suggests that some factors may affect organisms' decision rules.

Only few studies have up to now attempted to identify the individual decisions underlying the differential use of personal and social information during mate choice

(see Drullion and Dubois 2008, Kendal et al. 2009). Still, intrinsic factors, such as sexual experience (Ophir and Galef 2004) can affect the tendency to use social information when choosing a mate. To our knowledge yet, no study has examined the role of consistent inter-individual differences in behaviour, or "personalities", on mate-choice copying. Their influence yet deserves attention. Indeed, personality has already been found to influence the use of personal and social information in several species (Marchetti and Drent 2000; Nomakuchi et al. 2009). Thus, in a foraging context, reactive zebra finches are more likely to use personal information, i.e. search for food themselves in a producer-scrounger game (David et al. 2011a).

In addition to intrinsic factors, some extrinsic factors such as the reliability of demonstrators may affect individual decisions when facing different types of information. For instance, female guppies (*Poecilia reticulata*) are more likely to rely on the choice of older model females when choosing a mate (Dugatkin and Godin 1993). Similarly, propensity to copy conspecific's choice is influenced by demonstrator's quality in sailfin mollies (*Poecilia latipinna*) (Hill and Ryan 2006). Whereas body condition has been found to affect sexual preferences in many species (Cotton et al. 2006), nothing is known about the differential reliability of demonstrators varying in body condition. Still, females varying in body condition differ in their selectivity and sexual preferences in some species (Griggio and Hoi 2010), including the zebra finch (Burley and Foster 2006). The possibility thus remains that demonstrators' reliability may vary as a function of their condition.

The present study was then designed to evaluate the joint influence of an intrinsic factor (female's personality) and an extrinsic factor (demonstrator's body condition) on the tendency to use social information in a mating context using a classic mate-choice copying procedure (Galef and White 1998). We used the zebra finch as a model organism. This passerine bird is regularly used in studies of personality (David et al. 2011a,b), mate choice (David & Cézilly in press) and social information use (Swaddle et al. 2005; Drullion and Dubois 2008).

7.3. METHODS

7.3.1. Biological model

The zebra finch is a highly dimorphic monogamous passerine bird. Individuals live in large colonies in the wild (Zann 1996), suggesting that the use of social information may be relatively cheap and widespread in this species (David et al. 2011a). Our captive stock was kept in a breeding room where temperature was maintained at 22±2°C and the photoperiod was 13:11 h light:dark cycle (0730am-0830pm) with a 30-min period imitating dawn and dusk with increasing and decreasing light intensities in the morning and evening. Hundred and seventy-five wild-type, virgin but sexually mature males and females were kept in home cages (60×30×33 cm), by unisex flocks of two or three birds, before the experiments. Each individual was identified with an orange numbered ring (AC Hughes, Hampton Hill, UK; size XF). Orange is neutral towards female mating preference in zebra finches (Burley et al. 1982). Birds were provisioned with millet seeds, cuttlebones and water ad libitum. At the end of the experiment, birds were kept in groups of two to be used in subsequent studies. The experimental procedures were in agreement with the ethical requirements of the Université de Bourgogne.

7.3.2. Assessment of personality traits

Birds were food-deprived for one hour before each personality trial, except for obstinacy, to control for feeding motivation. All tests were performed on individuals kept single, except for aggressiveness. Detailed information concerning experimental apparatus and methodology can be found in David et al. (2011b), from which data on the personality of birds used in the present study were drawn.

Aggressiveness Aggressive behaviour was assessed within flocks of six birds in large cages (100×50×50 cm). Experimenters placed a unique feeder allowing only one bird

to feed at a time at the extreme side of the cage. The individual number of initiated aggressive acts was then recorded using a miniature camera (Typhoon Easycam) and used as an index of aggressiveness.

Activity Intrinsic activity levels were video-recorded (JVC Everio GZ-MG20) in home cages, immediately before neophobia tests. Individuals had no access to any food source during the trial. Following the time-sampling technique (Martin and Bateson 1993), experimenters assigned a score of 1 if the birds had moved between two perches or on the ground of a distance equivalent to two perches during the last five seconds, during a 10-min trial. If they stayed still, birds were assigned a score of zero.

Neophobia After the food-deprivation period, an unfamiliar object (small bag or soccer figurine) was introduced in the home cage at 10 cm from a unique feeder. Behaviour was then video-recorded for 15 min. The following variables were quantified: latency to perch near the feeder, latency to reach the feeder and take seeds, number of times the bird came feeding, number of times perched near the feeder and amount of time spent feeding. A Principal Component Analysis (PCA) was carried out with all these variables to synthesize them into a single value of neophobia. Corresponding eigenvectors can be found in David et al. (2011b).

Exploratory tendencies Individual exploratory tendencies were assessed in a large cage (140×140×70 cm) with which birds were unfamiliar. This cage had opaque walls, a clear Plexiglas ceiling and comprised five artificial trees each with four small branches. Behaviour inside the apparatus was recorded during 1 h with a video-camera placed 1 m above it. During analysis, the cumulative number of movements between trees and between branches of a single tree was quantified.

Startle test Latency to resume foraging after a stressful event was assessed. Experimenters placed a unique feeder in the home cage and two washers wedged between the feeder top and its trap door above it, linked with a fin thread to the outside of the room. Experimenters gently pulled the thread when the individual started feeding, creating vibrations on the feeder and a brief sound, which successfully frightened the bird off the feeder. Latency to resume foraging after that startle was then recorded live using a stopwatch through a miniature video-camera linked to a monitor outside the room.

Obstinacy Individuals were caught and put on a flat surface below a small landing net (20×15 cm). Number of hops and escape attempts was recorded during 30 sec as a measure of struggling intensity, thereafter called obstinacy. This manipulation was done by M.D.

7.3.3. Mate-choice procedures

Mate-choice apparatus consisted in a large cage (120×30×33 cm) divided into three sections (Fig. 7.1.a). Two males, unknown from the focal female, were randomly assigned to each of the stimulus-sections. The focal female was placed in the central section for a 5-min acclimation period. Trials were then video-recorded for 1 h. Male position was reversed after 30 min to avoid any side effects. Five minutes of acclimation were allowed to individuals to recover from this manipulation. All individuals had access to food and water during the trial. During analysis, female position was recorded every 10 sec following the time sampling technique (Martin and Bateson 1993, David and Cézilly in press). Following Rutstein et al. (2007), "active" and "passive" female postures were distinguished. To score an active posture, the focal female had to be observed facing in the direction of the male, standing on the closest perch near him. If the female was facing in the other direction

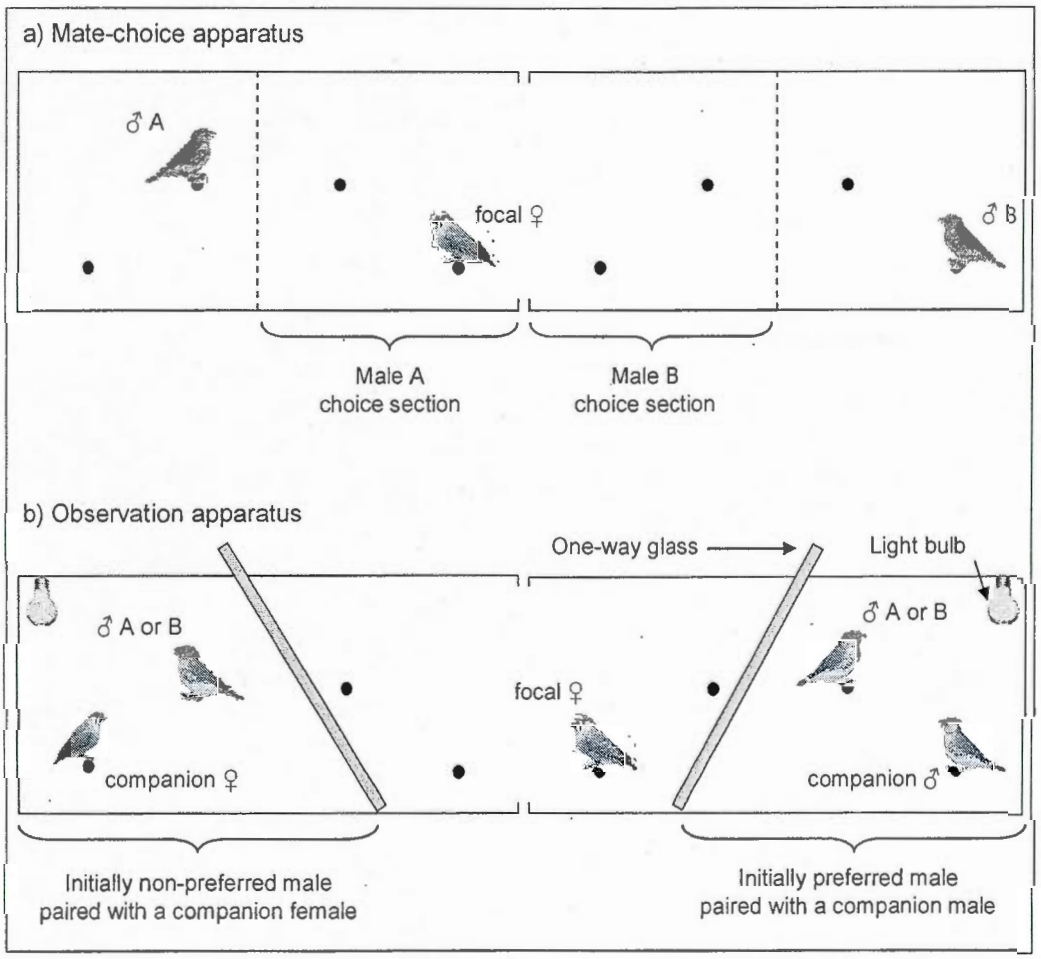

Figure 7.1. a) Mate-choice apparatus. The dashed lines correspond to the wire meshes. The focal female is presented here in a passive posture. Preference score for each male was assessed following the time sampling method from the number of times observed in an active posture (see methods and results sections). b) Observation apparatus. During six days, the focal female can observe the initially preferred male paired with a companion male and the initially least preferred male paired with a companion female. One-way glasses prevented males from interacting with focal females.

or standing on a more distant perch, her posture was recorded as passive. A preference score for stimulus-male was inferred from the number of times the focal

female was observed in both passive and active postures in each choice section, and a second one from the number of times the focal female was observed in active postures only.

The day following mate-choice trials, individuals underwent a 6-day period of observation during which the initially preferred male was paired with a companion male. The initially least preferred male was associated with a companion female to simulate a pairing event (Fig. 7.1.b). This experimental design follows the common procedure used to investigate mate-choice copying through preference reversal in several species (Galef and White 1998; Doucet et al. 2004; Godin et al. 2005). During this observation phase, one-way glasses replaced wire meshes of previous mate-choice apparatus (Fig. 7.1.b), enabling focal females to see the two pairs without being seen. This artefact also prevented males from same-sex pairs from being overtly aggressive towards each other because of the focal female's presence, and from directly courting her. One-way glasses were arranged in an oblique manner to minimize the interaction between a given male and his own image. Although some however did, these reactions became nonexistent after the second observation day. At the end of the observation period, individuals were removed from the apparatus and placed back in their home cage.

The day following the end of the observation phase, focal female's final preference for both initial males was measured following the same initial mate-choice procedure.

Control experiment To assess the possible role for an intrinsic evolution of preference which may have occurred out of any influence of the companion female, we performed the same entire procedure with 16 additional females but replaced companion females by companion males during the observation phase (Doucet et al. 2004).

7.3.4. Data analysis

Forty-one females composed the experimental group while 16 composed the control one. In a previous study, David et al. (2011b) showed that exploration tendencies, neophobia, reaction to a startle and activity were related each other, thus forming a behavioural syndrome. We then used the Personality Synthetic Values (PSV), which was computed by David et al (2011b) through a PCA reducing the personality traits constituting the behavioural syndrome to a single value per individual. Corresponding eigenvectors can be found in David et al. (2011b). Individuals defined by a high value were more exploratory, active, bolder and quicker to resume feeding after the startle. They were therefore categorized as "proactive", whereas individuals displaying lower values were categorized as "reactive" (David et al. 2011b).

The evolution of the focal female's preference was quantified from the change in preference score for the initially least preferred female. The evolution of the focal female's preference was thus computed as the difference between the final average score for the initially least preferred male and the initial average score for the same male, then divided by the initial average score for the initially least preferred male. The resulting variable was thereafter called the index of preference evolution. Positive values indicate that the focal female increased her preference for the initially least preferred male, and then relied to some extent on social information during the final mate-choice trial. Conversely, negative values indicate that she still increased her preference for the initially preferred male. We decided not to set a preference criterion under which females would have been discarded because of a presumed lack of sexual motivation (Rutstein et al. 2007), as this could lead to a bias in females used based on their personality (see David and Cézilly in press).

We evaluated the repeatability of preference scores using Pearson's correlations and Spearman's when data were not normally distributed. The evolution of preference for the least preferred male was compared between treatment groups and to a null evolution of preference using two-tailed t-tests. The relationship

between the evolution of preference and PSV, focal females' BCI or companion females' BCI was analyzed through an information-theoretic approach (Burnham and Anderson 2002; Garamszegi 2011) by comparing the AICcs of a subset of potential models (Hegyi and Garamszegi 2011). We chose to use AICcs, which are derived from AICs but are adjusted for small sample sizes, as the number of focal females used in the present study was low compared to the number of parameters computed in the most complex model (<< 40; Symonds and Moussalli 2011). We used the 'aictab' function of the "AICcmodavg" R package to compute and sort the different models by increasing values of AICcs. Models were considered to significantly differ from each other when their AICcs differed of at least 1. This analysis also brings out AICcs' weights, which can be assimilated to the probability of a given model to be the best approximated model (see Symonds and Moussalli 2011 and references therein), and evidence ratios, which are estimates of how much more likely the best model is compared to another specific model of the subset (Symonds and Moussalli 2011). Finally we computed each fixed effect's weight by summing the AICc weights of the models within which they appeared (Symonds and Moussalli 2011). These weights are used to rank each predictor as function of their importance in the models of the subset. For some demonstrators we had no data on their BCI, reducing our sample size to 26 in analyses where this variable was involved. We used JMP 5.0.1 software (SAS Institute, Cary, NC) and R 2.13.0 (R Development Core Team 2011) for statistical analyses. Data were log, square-root or boxcox transformed to reach normality when needed.

7.4. RESULTS

Overall, preference scores in an active posture were repeatable across the two initial mate-choice trials and the two final trials whereas preference scores in both passive and active postures were not (Table 7.1.). Preferred and least preferred males were

then identified based on the active posture preference scores thereafter (Rutstein et al. 2007). The evolution of preference for the initially least preferred male as well as other computations of preference were also thereafter based on active postures scores.

Preference scores for the least preferred male did not significantly differ between initial and final trials (Table 7.2.), both in the control (paired t-test: t_{15}=-0.29, P=0.77) and in the experimental group (t_{40}=0.49, P=0.63). This indicates that the evolution of preference for the initially least preferred male did not significantly differ from a null evolution in either group (Table 7.2.). Moreover, the evolution of preference for the initially least preferred males did not significantly differ between the control and the experimental group (t_{55}=-0.13, P=0.90). The distribution of the index of preference evolution is shown in figure 7.2. Females from the experimental group showed higher preference scores for the preferred male during initial tests than

	Experimental group		Control group	
	r	*P*	*r*	*P*
Initial trials				
Active postures	**0.37**	**0.008**	**0.58**	**0.007**
Passive & active postures	0.01	0.47	-0.11	0.67
Final trials				
Active postures	**0.36**	**0.01**	0.36	0.08
Passive & active postures	-0.07	0.67	0.25	0.17

Table 7.1. Repeatability of female preference scores during initial and final trials as a function of the type of posture (active or passive), in both the experimental (N=41) and the control group (N=16). Pearson's correlations were performed, except for final trials' analysis in both passive and active postures, for which Spearman's correlation coefficients are given. Significant or close to significance values are highlighted in bold type.

Groups	Preferred male score		Least preferred male score	
	mean±95% CI	%	mean±95% CI	%
Experimental				
Initial trial	121.1±18.3	33.6	43.0±10.1	11.9
Final trial	111.3±24.2	30.9	50.3±15.9	14.0
Control				
Initial trial	74.0±30.1	20.6	29.7±16.4	8.2
Final trial	67.7±28.3	18.8	26.9±12.5	7.5

Table 7.2. Preference scores for the two stimuli-males for initial and final trials and within both experimental (N=41) and control (N=16) groups. Scores were obtained through time sampling as the number of times the female was observed facing either male. Scores are given as mean (calculated across all birds from the same group) ± 95% Confidence Interval (CI). The column '%' indicates the percentage of occurrences that the female was observed facing either male. Overall, females from the experimental group showed higher preference scores during initial trials than females from the control group (see results)

females from the control group (t_{56}=-2.95, P=0.005; Table 7.2.).

Model computation indicates that the Minimum Adequate Model (MAM) has an AICc weight of 0.36 and significantly differs from the second-best model (ΔAICc = 2.05) with an evidence ratio of 2.79 (Table 7.3.). Moreover, MAM also differs from the null model (ΔAICc = 2.24). MAM only contains "demonstrator's BCI" as a predictor (Figure 7.3.; Table 7.3.). Variables' weights are as follow: "demonstrator's BCI" = 0.70; "PSV" = 0.34; "focal females' BCI = 0.27. Thus the evolution of preference negatively correlates with companion females' BCI (r_{24} = -0.41, P = 0.037; Figure 7.3.), such that the evolution of preference for the least preferred male

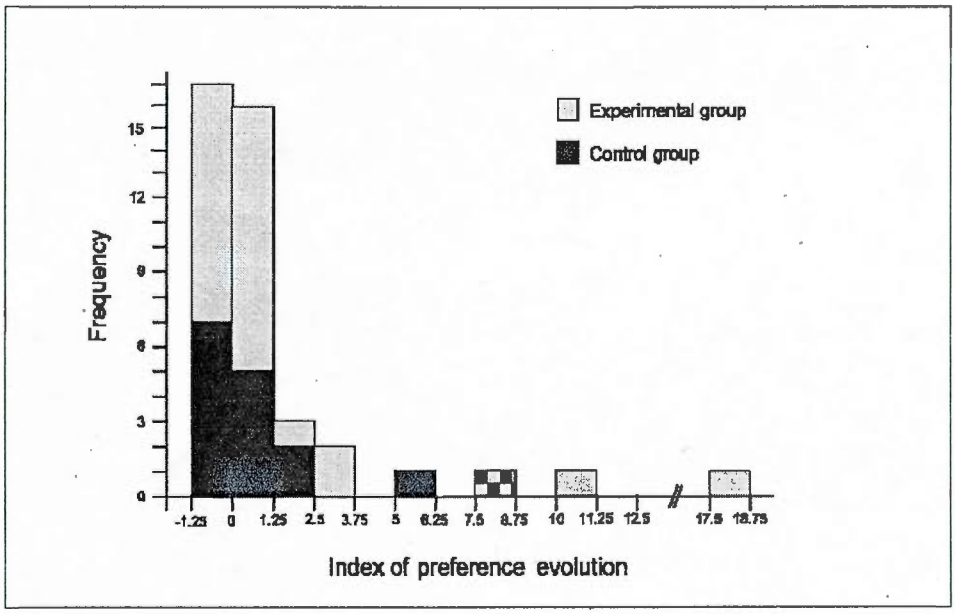

Figure 7.2. Frequency distribution of the index of preference evolution. Positive values correspond to females that increased their preference for the initially least preferred male while negative values correspond to females that decreased their preference for the initially least preferred male. The index was thereafter boxcox-transformed to reach normality for the purpose of statistical analyses. The mixed black and grey bar corresponds to two individuals coming from each group

was more pronounced when companion females were in poor condition.

7.5. DISCUSSION

Our study fails to show any evidence that females increase their preference for an initially least preferred male after watching him paired with another female. Indeed, the observed departure from a null evolution of preference has been found non-significant. Moreover, this evolution does not differ from the average evolution calculated from individuals of the control group, confirming previous studies (Doucet

	Candidate models	k	AICc	ΔAICc	AICc wt	ER
1	[DBCI]	3	89.71	0.00	0.36	
2	[DBCI] + [PSV]	4	91.76	2.05	0.13	2.79
3	[DBCI] + [FBCI]	4	91.93	2.21	0.12	3.02
4	Null	2	91.95	2.24	0.12	3.06
5	[PSV]	3	92.30	2.59	0.10	3.65
6	[FBCI]	3	94.29	4.58	0.04	9.87
7	[DBCI] + [PSV] + [FBCI]	5	94.42	4.71	0.03	10.52
8	[DBCI] + [PSV] + [DBCI*PSV]	5	94.60	4.88	0.03	11.49
9	[DBCI] + [FBCI] + [DBCI*FBCI]	5	94.71	4.99	0.03	12.15
10	[PSV] + [FBCI]	4	95.00	5.28	0.03	14.04
11	[PSV] + [FBCI] + [PSV*FBCI]	5	95.81	6.10	0.02	21.10

DBCI: Demonstrator's Body Condition Index FBCI: Focal female's Body Condition Index PSV: Personality Synthetic Value

Table 7.3. Computation of the candidate models built to explain the evolution of preference for the least preferred male as a function of three fixed effects: demonstrator's BCI, focal female's BCI and PSV. "k" indicates the number of parameters in the model, "ΔAICc" corresponds to the difference between any model's AICc and the AICc of the best approximated model. Models are considered to significantly differ when ΔAICc > 1. AICc weights ("AICc wt") can be assimilated to the probability for a given model to be the best approximated model. Evidence Ratios ("ER") are estimates of how much more likely the best model is compared to another specific model of the subset

et al. 2004). Overall, the occurrence of mate-choice copying within populations remains a highly debated topic with contrasted results between studies (Dugatkin and Godin 1993; Vukomanovic and Rodd 2007). The question of the importance of mate-choice copying in a monogamous species like the zebra finch thus remains open (Vakirtzis and Roberts 2010). Indeed, Swaddle et al. (2005) demonstrated that it takes

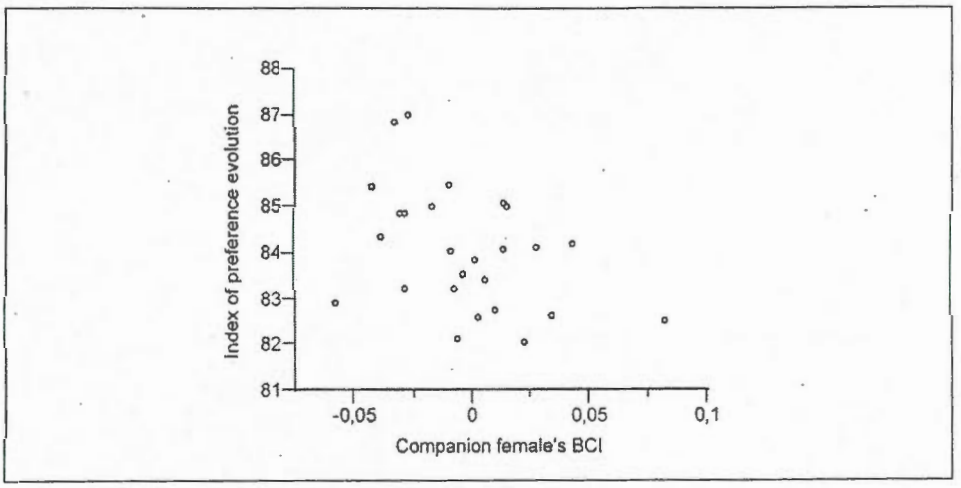

Figure 7.3. Relationship between the index of preference evolution and the Body Condition Index (BCI) of the companion female. Focal females increased their preference for the initially least preferred male when companion females was in poor condition. BCIs were obtained from the residuals of the regression of $\log_{10}$ (body mass) on $\log_{10}$ (tarsus length) (see methods). Y-axis values were boxcox-transformed to reach normality

a two-week observation period for females to express a significant preference towards the male from the heterosexual pair. Conversely, the observation period lasted only six days in the present study, which could explain why we found no evidence for mate-choice copying. In their study, Swaddle et al. (2005) used the amount of time that focal females spent in courtship display to assess their sexual preference, which make their results not quantitatively comparable to ours. Doucet et al. (2004) showed in their experiment that females from both experimental and control groups significantly increased their preference for the initially non-preferred males (from 17% to 42% in the experimental group and 14% to 46% in the control one). In the present study, we also found that birds from the experimental group increased their preference for the initially least preferred males (12% to 14%), although this evolution was not significant, while females from the control group did not (8% to

7%). Moreover, preference scores for the preferred male were higher in Doucet et al. (2004)'s study. This could be because their apparatus was rather simple and offer no other possibility to focal females than facing either male. In our study, the mate-choice apparatus comprised four different perches (only two of them were used to calculate active preference scores (see Methods), and birds were given food and water during trials, which consumption may have reduced the time dedicated to courtship and mate sampling activities.

We found no effect of overall personality, computed here as a personality synthetic value, on female tendency to increase their preference for the initially least preferred male. Thus, contrary to previous studies carried out in a foraging context (Marchetti and Drent 2000; David et al. 2011a), individuals with different personalities do not seem to differentially use personal vs. social information when assessing different mating options. The inability to identify the causes of between-individual variation in the tendency to rely on conspecifics in a sexual context may be linked to the relative lack of knowledge of what constitutes relevant information to organisms when they choose a mate (Jennions & Petrie 1997) compared to when they forage. Indeed, females of the same population commonly show variation in their mate sampling tactic (David & Cézilly in press) or their sexual preference (Brooks & Endler 2001). Moreover, quickly assessable male traits such as morphology may interact with behaviour (Godin and Dugatkin 1996) such that the question of what information influences individual decisions often remains unanswered. In contrast, animals are classically expected to maximise their intake rates by preferring relative most profitable options or food patches in foraging studies (Illius et al. 1999; van Gils et al. 2003). The factors providing information on which organisms base their decisions may thus be easier to determine in a foraging than in mate-choice context. Further investigations should thus be aimed at identifying the interaction between male characteristics and social information use (Godin et al. 2005; Alonzo 2008; Côté, Dubois, Witte, Giraldeau in preparation).

In some species, the tendency to copy conspecifics' mate choice is linked to the characteristics of the demonstrators, i.e. companion individuals (Waynforth 2007). For instance, in sailfin mollies, females rely more on information provided by high-quality conspecific females to choose a mate (Hill and Ryan 2006). In guppies, young females are more likely to copy the choice of older females (Dugatkin and Godin 1993). Here we provided evidence that copying was negatively related to the condition of companion females, such that poor-condition companion females may have a larger influence on the use of social information by focal females. Alternative explanations may account for this pattern. First, it is known that female preference can be condition-dependent (Cotton et al. 2006), such that females may benefit to rely on the choice of females in the same condition as theirs. A recent study conducted with house sparrows (*Passer domesticus*) found that poor-condition females showed more pronounced mate preferences (Griggio and Hoi 2010). Their choice could thus be more reliable for naive females in a social context. However, we found no interaction between focal females' BCI and companion females' BCI in the present study. In zebra finches, females in experimentally reduced condition are less selective (Burley and Foster 2006). These individuals may thus be unlikely to provide useful information to naive conspecifics. The manipulation of condition consisted in wing-clipping in Burley and Foster (2006). The influence of this procedure on the subjective experience of organism regarding their condition and the decisions they subsequently adopt however may differ from the one of variation in residual body mass, which is a more common indicator of condition in avian studies (Schamber et al. 2009). A second possibility to explain reported results is that focal females may be more successful when competing or physically interacting with poor-condition females, for instance when courting a mate. Females may thus afford to seduce and attract a male paired to a poor-condition conspecific with only minor risks of retaliation from her. Further research is yet needed to understand to which extent and why variation in the demonstrator's characteristics influences mate-choice copying.

From a methodological point of view, our results argue in favour of the use of active postures in front of males to assess female preference in spatial association tests. Indeed, active-posture preference scores were found more repeatable than passive and active postures taken together. Yet, one can notice that total time spent near a male, irrespectively of the posture adopted, has already been found repeatable and used in previous studies (Doucet et al. 2004; David and Cézilly in press). To conclude, we propose that both postures, along with displaying activity (Swaddle et al. 2005), should systematically be recorded during mate-choice experiments through spatial association so that the adequate measures can later be used depending on their reliability.

To conclude, the present study provides no additional evidence for mate-choice copying in a monogamous species like the zebra finch. This finding is comparable to some previous studies which used similar protocols (Doucet et al. 2004; Vukomanovic and Rodd 2007). Yet we found that the condition of demonstrators could affect female tendency to prefer the initially least-preferred male, such that poor-condition demonstrators would provide more reliable information about a potential mate. Further research should be designed to identify what benefits females may gain by relying on a specific type of demonstrator.

7.6. ACKNOWLEDGMENTS

We thank Sébastien Motreuil for his assistance during bird care and the building of the experimental devices, Mark Gillingham for statistical advice, and Elise Melloul for assistance during the experiment. This work was funded with a Ph.D. grant to M.D. and a master honorific grant to Y.A., both provided by the Conseil Régional de Bourgogne

ARTICLE VII

PERSPECTIVES ON ANIMAL PERSONALITY AND SEXUAL SELECTION

Morgan David, Luc-Alain Giraldeau & Frank Cézilly

8.1. ABSTRACT

Both sexual selection theory and the concept of animal personalities have recently placed emphasis on consistent individual differences in behaviour. However, the extent to which they can be related has been neglected so far. In the present paper, we review the existing evidence linking personality and sexual selection. We show that the study of alternative reproductive tactics may prove useful to investigate the proximate mechanisms of personality. Additionally, relationships between personality and fitness can be used to predict female preferences, and *vice-versa*. The joint study of personality and sexual selection represents a promising avenue of research for studying the maintenance of personality variation through sexual selection and the influence of personality on sexual behaviours.

8.2. NATURAL SELECTION, SEXUAL SELECTION AND PERSONALITY

Over the last decade, the concept of animal personality has become one of the most stimulating issues in the field of animal behaviour (Bell 2007; Réale et al. 2007). Behavioural ecologists have defined animal personality as a set of intrinsic tendencies, such as boldness or exploration, driving individual consistent behaviour across contexts and over time but differing among individuals of a population (Sih et al. 2004a; Bell 2007). Personality is linked to fitness in a large range of species (Smith & Blumstein 2008) and is heritable (Drent et al. 2003; van Oers et al. 2004), suggesting that it can evolve through natural selection (Quinn et al. 2009). From a theoretical viewpoint, the rigidity of personality traits across contexts is challenging the classic thinking in behavioral ecology that behaviour is infinitely plastic (Sih et al. 2004a). It calls for the investigation into inter-individual variation in behaviour and the factors that maintain it (Sih et al. 2004a). Tracking the role of personality in several different situations is required to provide a full understanding of individual success across contexts. Personality has rarely been studied in a sexual selection context (Godin & Dugatkin 1996; van Oers et al 2008). The extent to which personality and sexual selection are linked and the possible consequences of this relationship remain poorly investigated, despite evidence for sex differences in personality (Smith & Blumstein 2008; Schuett et al. 2010). Thus, the role of sexual selection in the evolution of personality remains poorly explored, although it is a major selective force on male traits. Similarly, few studies emphasize the extent to which personality could explain the common variation observed in mating behaviours (Kortet & Hedrick 2007; van Oers et al. 2008; While et al. 2009). Yet, personality is usually highly consistent within individuals and can influence subsequent behaviours in the long term, leading to within-population differences.

In this paper we will briefly review studies linking animal personality and sexual selection, and insist on the resulting ecological and evolutionary consequences. More precisely, we will highlight both how the widespread observed

variation in mate choice (Jennions & Petrie 1997; Widemo & Saether 1999) could be explained by variation in personality and how sexual selection processes may contribute to the maintenance of variation on personality traits (Dingemanse & Réale 2005; Schuett et al. 2010). Moreover, we will describe how personality and behaviour in general differ by nature from morphological traits as targets of mate choice, and what consequences this may have on their evolution by sexual selection. We will then to propose a framework to infer the diversity of female preferences from the fitness consequences of personality and vice versa.

Sexual selection is generally studied as two separate processes, *i.e.* intrasexual and intersexual selection because the outcomes of these processes are quite distinct. Intrasexual selection leads to the evolution of armaments that function to acquire mates via interference competition, or ornaments designed to maximize the encounter with and locate members of the opposite sex. Intersexual selection generally leads to the evolution of ornaments in one sex in response to choices for that trait in the other sex. Because of this we propose to investigate the link between personality and sexual selection separately in both processes.

8.3. ALTERNATIVE REPRODUCTIVE TACTICS AND THE PROXIMATE MECHANISMS OF PERSONALITY

The development of secondary sexual characters used in male-male competition is traditionally associated with strong directional selection towards a maximal trait value that allows one to win contests and then monopolize females (Parker, 1983). However, in some species, males also adopt alternative tactics to gain access to mates (Oliveira et al., 2008), as illustrated by the "territorial-sneaker" system of side-blotched lizards, *Uta stansburiana* (Sinervo & Lively 1996) or garter snakes, *Thamnophis sirtalis parietalis* (Shine et al. 2003). It is often implicitly considered that these alternative reproductive tactics (ART) are associated with a range of

distinct behaviours between different phenotypes. In a study on captive lizards (*Eulamprus heatwolei*), territorial males were found to be more wary and less likely to leave a shelter in search of foraging opportunities than floater males, or sneakers (Stapley & Keogh, 2004). In tree lizards (*Urosaurus ornatus*), non-territorial males were more wary towards predators and stayed hidden longer in the shelter, as opposed to territorial males (Thaker et al. 2009). Those links between ART and some personality traits are noteworthy for several reasons: first, it suggests that personality traits may have co-evolved with discrete reproductive strategies to yield efficient and adaptive reproductive tactics. This hypothesis predicts that variation in personality traits can be maintained through the correlated effects of intra-sexual selection on ART. Second, personality consistency itself may be a target of natural selection (see Schuett et al. (2010) for a similar hypothesis with sexual selection). Indeed, it might be detrimental to the efficiency of the reproductive tactic to be associated with inconsistent behaviours.

Finally, proximate mechanisms can be defined as all those ontogenic or physiological mechanisms involved in the development and maintenance of a behavioural or morphological trait. The existence of ART leaves open the question of the proximate mechanisms involved in the development and maintenance of such distinctive reproductive behaviours within a species (Oliveira et al. 2005, 2008). In some cases, hormones such as corticosterone, testosterone, or neuropeptides such as arginine vasotocin mediate switches between different ART phenotypes (Knapp et al. 2003; Oliveira et al. 2005). Interestingly, testosterone and corticosterone titres are linked to personality in some birds (Kralj-Fišer *et al.* 2007; Martins *et al.* 2007; Spencer & Verhulst 2007). This suggests that the same proximate determinants could be involved in the development of both ART and personality (figure 8.1.; Semsar et al. 2001; Ten Eyck 2005; see Dewan et al. 2008 for a between-species comparison). Studying personality in the context of ART could then help unravel some of its developmental and physiological determinants.

As previously seen, ART classically consist in one category of individuals

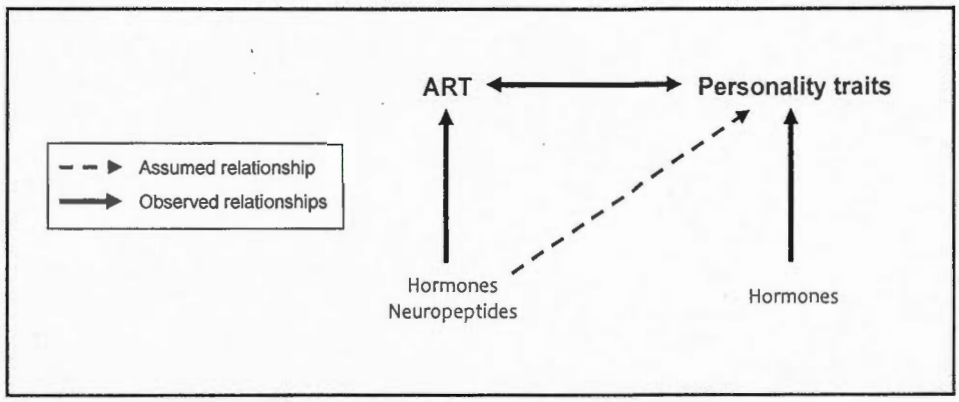

Figure 8.1. Multiple relationships between ART, personality and their proximate mechanisms.

being territorial to attract mates and the others acting as sneakers and trying to parasitize reproductive events. In some species, individuals play a fixed tactic throughout lifetime whereas in others they can consecutively switch from one tactic to another (see fig. 1 in Oliveira et al. 2005). If personality co-evolved with ART in those systems, it is expected to vary as a function of the tactic adopted by an individual. It would then be of great interest to discover "reversible" ART (*i.e.* different tactics adopted consecutively by the same individual throughout lifetime) influenced by personality. As individuals switching across different ART requires vast hormonal and neuro-hormonal reorganization (Oliveira et al. 2005), their effects on personality *via* the same mechanisms or not may be correspondingly considerable. Although consistency is the basis of the definition of personality (Réale et al. 2007), we would expect in those cases personality to vary as individuals switch tactics. Indeed, personality has mainly been investigated in species for which reproductive and even life-history tactics were fixed, such as great tits (*Parus major*; Dingemanse et al. 2002) or sticklebacks (*Gasterosteus aculeatus*; Dingemanse et al. 2007). This bias could explain why behavioural consistency now is the basis of the definition of

animal personality. Contrary to the view that personality represents an arbitrary background influencing individual behaviour, this hypothesis would lead us to consider personality as part of an adaptive set of behaviours co-evolving with life-history tactics and trajectories (Biro & Stamps 2008). Personality consistency should be reconsidered if personality traits show intra-individual variation when organisms switch from one ART to another.

8.4. HOW CAN FEMALES ASSESS MALE PERSONALITY DURING MATE CHOICE?

Time constraint is assumed to be an important factor influencing which cues are used by females when choosing a mate (Sullivan 1994). Hence, morphological traits, quickly assessable, are more likely to be used on leks or in any other system in which female sampling is time-limited. On the contrary, behavioural cues can hardly be assessed under short time scales. Mate choice based on behavioural traits or personality then requires specific dispositions such as monogamous mating systems, repeated interactions within a pair or a group, facilitating eavesdropping to name just a few of them (Danchin et al. 2004). However, this time-consuming sampling process may be overridden in a system in which a behavioural trait is related to a morphological character or to any sensory cue. In this case, a choice based on a behavioural or personality trait could be indirectly realized through a choice based on a sensory cue. Several lines of evidence indicate that this process may be functional in a "personality-sensory cue" system. In numerous species, one coloured morph is commonly more aggressive and dominant over the other (*e.g.* in lizards: Sinervo & Lively, 1996; Stapley & Keogh, 2004; Thaker et al. 2009; in birds: Pryke & Griffith 2006; in fish: Kingston et al. 2003, Dijkstra et al. 2009; *see* Pryke 2009 for a review of the relationship between red coloration and aggressiveness and dominance across taxa), though females can indirectly select for personality through a choice based on

morphology. In other species, variation in one sensory cue is related to variation in personality traits. In male guppies, boldness towards predators has been related to visual conspicuousness (Godin & Dugatkin 1996). In field crickets (*Gryllus integer*) and cockroaches (*Nauphoeta cinerea*), females can discriminate aggressive and dominant males from subordinate ones using olfactory cues (Moore et al. 2001; Kortet & Hedrick 2005). Boldness can be inferred from time spent courting females in male fiddler crabs *Uca mjoebergi* (Reaney & Backwell 2007) and field crickets (Hedrick 2000). Finally, singing behaviour is linked to aggressiveness and dominance in male black-capped chickadees, *Poecile atricapillus* (Hoeschele et al. 2010; and references therein), to boldness in male collared flycatchers, *Ficedula albicollis* (Garamszegi et al. 2008), and exploratory tendencies in great tits (Naguib et al. 2010). All these studies demonstrate that personality traits could be sexually selected through a choice based on sensory cues, while overriding time-consuming sampling. Insofar as mate personality is an important component of female fitness, large sampling costs can be considerably reduced in a "personality-sensory cue" system. Sexual selection on these behavioural traits may then not be solely restricted to specific situations as described above, and could potentially be more widespread than expected without this personality-sensorial cue system.

8.5. FEMALE CHOICE FOR MALE PERSONALITY

Investigations on sexual selection through female choice traditionally focused on sexual preferences for morphological characters such as conspicuous colours or elongated feathers (Andersson, 1994). Few studies have investigated the role of male behaviour on female choice beyond classic courtship displays (Byers et al. 2010). For instance, behavioural compatibility between pair members, quantified by proximity, behavioural synchronization, allopreening, aggression, plays a crucial role in cockatiels *Nymphicus hollandicus* mating (Spoon et al. 2006). Hence, females are

more likely to search for extra-pair copulations and to switch mates when they are paired with a low-compatible mate (Spoon et al. 2007, see van Oers et al. 2008 for an opposite pattern in great tits). These studies show that behaviour can be a choice criterion, along with physical ornaments, and can play a significant role in mate choice. Similarly, some evidence demonstrate that personality can be a choice criterion in some species: tests on female preference for both boldness and amount of colour patches in the Trinidadian guppy (*Poecilia reticulata*) revealed that bright males were preferred over drab ones and that bold males, more prone to expose themselves to predation threats, were preferred over shy ones (Godin & Dugatkin 1996). Moreover, boldness was positively correlated with male visual conspicuousness. When bright and drab males were made experimentally more or less bold in front of females by simulating predator inspection, females preferred bold males, irrespective of their colour pattern, under predation risks, whereas they preferred bright males, irrespective of their predator inspection behaviour, when there was no risk (Godin & Dugatkin 1996). Conspicuousness therefore could be a reliable indicator of male quality through which females could get information on and select for male personality. As there are few opportunities in nature to assess male boldness towards predators, females would be more likely to use colour patterns as a proxy for boldness and a proximate criterion for mate choice (the "personality-sensory cue" hypothesis), as proposed in the previous section. Conspicuous ornaments therefore could have evolved as morphological correlates of personality in this species and convey indirect information on male quality. Further investigations on the relationship between personality, female choice and male ornaments are needed to explore the extent to which these findings apply to other systems.

In a study on field crickets (*Gryllus integer*), male display intensity was negatively correlated to risk-taking behaviour (Hedrick 2000). Hence, the more a male called to attract females, the more it was long to resume any activity after being threatened by a virtual predator. Singing males then compensated for their higher exposure to predation risks during courtship by being more cautious. In short,

extravagant singers were shy but preferred by females (Hedrick 1986). In this system, shy males were favoured by sexual selection whereas bold ones were favoured by natural selection because they were less likely to be detected by predators during courtship. Females can therefore contribute to the maintenance of variation on personality through mate choice, suggesting that personality can evolve by inter-sexual selection (Reaney & Backwell 2007).

These results demonstrate that personality can be a target of mate choice. The study of personality in a sexual context provides a good opportunity to investigate and highlight the forgotten role of male behaviour on female choice and mating preferences (Byers et al 2010). It also enables one to consider that extreme sexual morphological dimorphism may not be the sole route to sexual selection through mate choice (Box 8.1.).

8.6. FEMALE PERSONALITY AND MATE CHOICE

Inter-individual variation in mate choice and mating preferences is of prime interest to behavioural ecologists. Indeed, numerous studies highlight among-female variation in mate choice behaviour (Jennions & Petrie 1997), although all females of a given population are expected to exert the same selection pressures on male ornament. Identifying the causes and consequences of this variation would provide a major step towards the understanding of the co-evolution between male traits and female preferences. Several ecological and individual factors can affect inter-individual differences in mating behaviour (reviewed in Jennions & Petrie 1997, Holveck & Riebel 2009). However, the role of personality on female mating behaviour is just beginning to be explored. Thus, in zebra finches (*Taeniopygia guttata*), female personality influences selectivity, preference strength and preference repeatability (David & Cézilly, *in press*). Exploratory females show lower selectivity, and express less pronounced but more repeatable preferences towards males. This study

Box 8.1. Monomorphism and personality

Sexual selection is assumed to be of lower intensity in monomorphic species (Björklund 1984; Bridge & Nisbet 2004, *but see* Owens & Hartley 1998). It is taken to result from the absence of strong intra-sexual competition for mates and also to be a consequence of the absence of morphological cues available to females when choosing a mate (Byers et al 2010). As a consequence, sexual dimorphism has already been used as a proxy for sexual selection intensity (Ritchie et al. 2007). Low levels of dimorphism or ornamentation are thought to make male characteristics long to assess and more likely to be signalled by other cues (Sullivan 1994). Following this reasoning, behaviour could be, beyond morphological traits, alternative candidate targets of mate choice in monomorphic species (Sullivan 1994). Many studies show that females may appraise potential mates from their behaviour (in spotted sandpipers: Colwell & Oring 1989; in razorbills: Wagner 1991; in Humboldt penguins: Schwartz et al. 1999; in barnacle goose: van der Jeugd & Blaakmeer 2001; in kittiwakes: Helfenstein et al. 2003; in budgerigars: Spoon et al. 2006). All those cited species are sexually monomorphic. In crested tits (*Parus cristatus*), another monomorphic species, male ability to copulate repeatedly has been found to be correlated with body condition (Lens et al. 1997), suggesting that repeated copulations could be a way for females to continuously assess their mate's quality. In the black wheatear (*Oenanthe leucura*), also a monomorphic species, males carry quantities of stones to the nest before reproduction. It has been experimentally demonstrated that a pair's reproductive success is positively correlated to male initial effort (Soler et al. 1996). In this case, females would invest energy into the eggs as a function of their partner's initial investment. A meta-analysis would be useful to test the generalizability of the relationship between behaviour as a target of mate selection and decreased dimorphism between sexes. Compared to the stereotypic behaviours described above, individual personality present the advantage of being basically highly variable within populations, consistent at the individual level and related to

fitness. Thus, even if a "personality-sensory cue" could not be at work in monomorphic species, personality can be a reliable cue on which females may base their choice (Schuett et al 2010), in this type of species. To conclude, taking personality into account in mate choice studies could perhaps widen the role of inter-sexual selection to monomorphic species.

underlines the role of personality as a confounding factor biasing the interpretation of mate choice experiments. Moreover, it suggests that female personality could explain the observed inconsistencies between studies performed on different sets of individuals (Collins & Ten Cate 1996).

Unsurprisingly, some evidence shows that both female and male personality can act together and affect pairing patterns. In great tits, exploratory males preferred exploratory females during mate choice tests whereas less exploratory males did not show any clear preference (Groothuis & Carere 2005). The same pattern was found in zebra finches (W. Schuett, PhD thesis, University of Exeter, 2008). Exploratory females significantly preferred high- and medium-exploratory males, whereas less exploratory ones did not show any clear preference for a given male personality.

These results contribute to the identification of an additional individual factor influencing variation in mating behaviour (Jennions & Petrie 1997), and suggest that personality can explain a significant part of the commonly observed variation in mate choice studies. Moreover, male and female personality can interact in a complex way and lead to pairing patterns that are meaningful only when individual personality is taken into account.

Having described the conditions under which personality and sexual selection may be related and provided evidence that they are effectively tightly linked in practice, we can now turn to predicting the selection pressures acting on male personality and explain what the consequences for the evolution of personality are.

8.7. INFERRING FEMALE PREFERENCES FOR MALE PERSONALITY

Contrary to the traditional view of sexual selection acting on morphological characters, recent evidence suggests that the value of a potential mate does not only depend on its own intrinsic quality but also on the chooser's characteristics (Spoon et al. 2006; Holveck & Riebel 2009). Regarding personality, females of the same population could express diverging preferences towards the same males. This may lead to unusual but predictable selection pressures on the evolution of male characteristics. Determining both the shape of the personality fitness curves and the reproductive success of pairs with known personalities can be useful tools to predict female sexual preferences for male personality. Figure 8.2. represents two simple theoretical curves that could be obtained from an experiment designed to measure personality fitness. The X-axis, ranging from -1 to +1, corresponds to a personality trait's range of values. A fitness component, such as reproductive success or survival, defines the y-axis. Figure 8.2.a describes a situation where individuals with extreme personalities get low fitness. In figure 8.2.b, extreme-personality individuals acquire high fitness. If we consider that personality traits are heritable (van Oers et al. 2004), some predictions on female preferences can be drawn from the shape of the fitness curves. Females are expected to prefer mates offering the best perspectives in terms of offspring fitness. Thus, in the case illustrated in figure 8.2.a, females with an extreme personality value pairing with an opposite-personality male will produce high-fitness offspring. There should then be selection towards heterogamous preferences. This process would have consequences on the evolution of the personality trait: its variance should be reduced across generations through stabilizing selection resulting from heterogamous pairings. In the case illustrated in figure 8.2.b, extreme-personality females choosing similar males will produce high-fitness offspring. There should then be selection towards positive homogamy, or assortative mating (except for intermediate females). This pairing system would help maintain

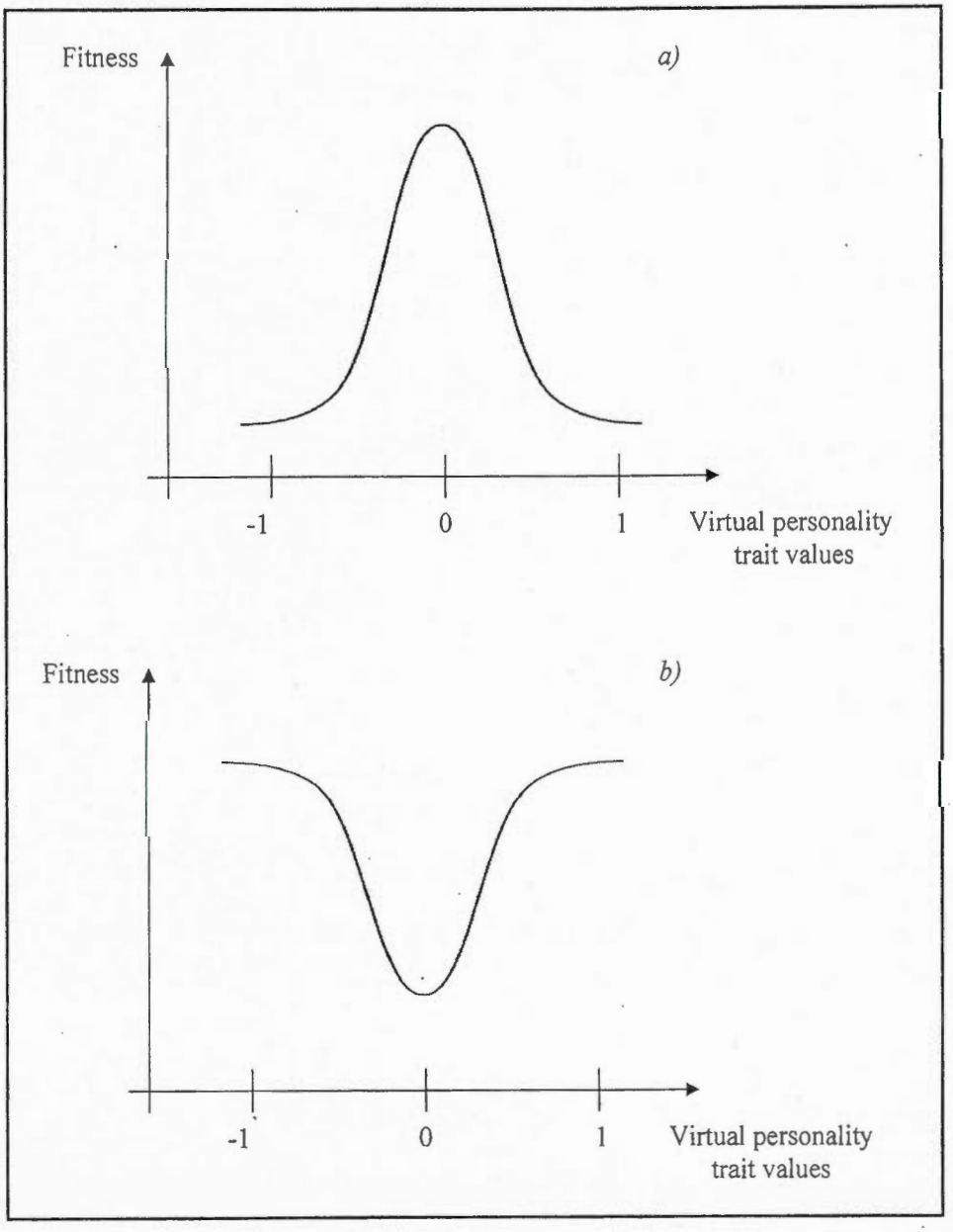

Figure 8.2. Virtual relationships between personality and fitness. Predictions on the direction of female sexual preferences can be drawn from this type of data.

variance on the personality trait through disruptive selection resulting in a decrease of heterozygote frequency (*i.e.* intermediate phenotypes) across generations (Kondrashov & Shpak, 1998). Actually, several studies already investigated the fitness consequences of personality within populations, or the reproductive success of pairs of individuals with known personalities, offering some possibilities to predict and assess the direction of female preference towards male personality (Box 8.2.).

8.8. CONCLUSION: A BIDIRECTIONAL APPROACH

Despite an increasing interest in inter-individual differences, the relationship between animal personality and sexual selection is just beginning to be explored. In this review we have considered some of the existing studies on this topic and pointed out some relevant perspectives. We have suggested that the link between personality and alternative reproductive tactics is a convenient system to investigate the proximate mechanisms of personality and to understand its adaptive nature. More studies are however needed to appraise the generalizability of this link.

Regarding mate choice, many studies emphasized a correlation between personality and a sensory cue. These "personality-sensory cue" complexes are convenient systems enabling females to select a mate for its personality while basing their choice on morphology. This system has the advantage of overriding any time-consuming sampling of male behaviour and facilitating the evolution of personality through inter-sexual selection.

Some studies pointed out that both female and male personality may affect mate choice outcomes. This urges us to take inter-individual differences into account in studies of mate choice. On the one hand, female personality can bias the interpretation of mate choice experiments, and on the other, male personality can be a target of choice, which does not follow the traditional mechanisms of ornament evolution through mate choice. While this type of study may prove highly useful to

Box 8.2. Determining female preferences through studies on personality's fitness

Several studies examined the fitness consequences of personality in terms of survival or reproductive success (Smith & Blumstein 2008). Predictions on the direction of female preferences for male personality can be inferred from this type of data. In a study on great tits, mating pairs composed of individuals of both similar and extreme personalities produced fledglings in better condition than other pairs (Both et al. 2005). These results fit our figure 8.2.b-scenario. In this system, extreme-personality females are expected to prefer males matching their own personality. During mate choice tests performed on the same species, fast-explorer males prefer fast-explorer females (Groothuis & Carere 2005). Instead, slow-explorer males did not show any preference for female personality. Although conducted on males, sexual preferences regarding mate's personality in part go in the direction predicted by the former study. A quantitative genetic analysis performed on great tits revealed that personality values such as shyness and slow exploration express genetic dominance over boldness and fast exploration (van Oers et al. 2004). This could explain why, as opposed to bold individuals, shy great tits do not show any preference for a given personality. Indeed, because of dominance effects, homozygous shy individuals could never produce something else than shy offspring. In a study on dumpling squids (*Euprymna tasmanica*), bold and intermediate females had a higher reproductive success when paired with a similar male than with dissimilar ones (Sinn et al. 2006). However, the success of shy females did not vary according to their mate's personality. In this case, bold and intermediate females should express a preference towards intermediate and bold males in order to maximize their reproductive fitness. The type of study described above can be useful for several reasons. First, predictions on the evolution of female preference for male personality can be inferred from personalities' fitness curves. Conversely, the direction of female preferences could be used to predict the relationship between personality and fitness, as far as females show adaptive preferences for male personality. Finally, the relationship between

personality and fitness has been found highly variable across years within studies (Dingemanse et al. 2004; Boon et al. 2007). Following our theory, this leaves open the possibility that females should show flexible and adaptive mating preferences across years. Maintenance of variation on sexually selected traits is currently a highly debated topic (Radwan 2008), and flexible adaptive mating preferences have been proposed and experimentally proved as a cause of within-individual variation in mating preferences (Chaine & Lyon 2008; Lehtonen & Lindström 2009). Variation in fitness consequences of personality thus provides an appropriate study subject to investigate the evolution of variable female mating preferences.

understand and predict the influence of personality on mate choice, it also demonstrates how personality can evolve through sexual selection.

Because of the link between personality and fitness, and insofar as it affects their reproductive fitness, females are expected to select males based on their personality. An interesting perspective lies both in the prediction of female preference for male personality according to the shape of the personality fitness curve and in the determination of this fitness curve based on female preferences. This method offers insights into the evolution of both female preference and personality.

To conclude, investigations linking personality and sexual selection are promise to add new perspectives to the study of sexual selection processes while considering the evolutionary origins of personality within a bi-directional approach.

CONCLUSION

Cette thèse de doctorat a été divisée en deux thématiques distinctes, permettant ainsi d'apprécier les liens entre la personnalité animale et les stratégies biodémographiques d'une espèce modèle en écologie comportementale : le Diamant mandarin. Nous avons en premier lieu établi un syndrome comportemental au sein de notre population captive en mettant en évidence les corrélations existant entre les cinq traits de personnalité évalués. L'étude de l'influence de la personnalité à travers deux différentes situations de compétition alimentaire a constitué la deuxième partie de cette thèse. Les résultats obtenus suggèrent que le lien entre personnalité et aptitude phénotypique pourrait être fonction du type de compétition. Enfin, la dernière partie a consisté à démontrer, de manière empirique, l'influence de la personnalité sur la mesure du choix du partenaire des femelles en conditions expérimentales ; et de manière théorique, à présenter les enjeux de l'étude conjointe de la personnalité animale et de la sélection sexuelle, en soulignant ses implications dans le maintien de la personnalité par sélection sexuelle et dans l'influence de la personnalité sur les comportements sexuels.

9.1. SYNDROME COMPORTEMENTAL CHEZ LE DIAMANT MANDARIN

La première partie de cette thèse a caractérisé un syndrome comportemental chez le Diamant mandarin *via* l'existence de corrélations entre des traits de personnalité classiquement étudiés (Dingemanse *et al.* 2002 ; Tobler & Sandell 2007). L'originalité de cette étude tient au fait que les rares travaux s'étant intéressés aux différences inter-individuelles de personnalité chez les Diamants mandarins ou chez d'autres espèces n'ont en fait porté que sur un ou deux traits (Spencer & Verhulst 2007 ; Schuett *et al.* 2009), délaissant la possibilité que certains d'entre eux aient pu évoluer indépendamment et ne pas être représentatifs de la personnalité globale des

individus. Nous avons donc pu déterminer dans quelle mesure différents traits de personnalités sont associés au niveau de notre population expérimentale de Diamants mandarins et si l'utilisation d'un seul trait dans nos expériences eut pu suffire à inférer des conclusions sur la personnalité globale des individus. Il est important de noter que certaines études ont récemment montré que les corrélations intra-populationnelles entre traits de personnalité pouvaient être dépendantes de certains facteurs écologiques, comme la prédation (Dingemanse *et al.* 2007), et être elles-mêmes les objets de la sélection naturelle (Bell & Sih 2007). Ces faits pourraient ainsi limiter la portée de la mise en évidence d'un syndrome comportemental au sein d'une population captive issue de conditions d'élevage forcément artificielles. La caractérisation d'un syndrome comportemental dans une situation donnée ne peut probablement pas être utilisée pour inférer l'existence de ce syndrome dans une autre situation. Mais pour autant nos résultats apportent quelques enseignements. Dans notre étude, la population de Diamants mandarins montrait un syndrome comportemental associant entre eux les traits de néophobie, d'exploration, d'activité et de prise de risque. De plus, le trait « d'obstination » ou « persévérance », défini comme le nombre de tentatives d'échappements lorsque l'individu est placé sous un filet, n'était quant à lui relié à aucun autre trait. Ces résultats nous offrent plusieurs enseignements. Tout d'abord, l'utilisation d'un seul trait de personnalité ne peut être *a priori* justifiée pour définir la personnalité globale des individus étudiés. Dans notre étude, la persévérance aurait pu être utilisée pour quantifier la personnalité globale de nos oiseaux et tenter d'être reliée à des stratégies biodémographiques diverses. Si cette démarche n'est pas erronée en soi, elle ne peut être élargie à l'influence de la personnalité globale de nos individus, de même que l'utilisation d'un trait intégrant le syndrome, comme l'exploration, ne peut prédire l'influence de la persévérance sur un tiers trait. La prise en compte d'un seul trait prenant part au syndrome peut seulement servir à prédire l'influence des autres traits du syndrome, mais pas la personnalité dans sa globalité. Encore une fois, ces inférences ne sont fondées que pour l'étude de la personnalité dans un seul type de condition. Notre étude a été conduite dans un

contexte standardisé qui peut nous permettre de prédire que certains traits de personnalité seront associés entre eux lors d'études en laboratoire. Rien ne nous permet toutefois de prédire ces liens dans d'autres contextes, comme des études *in natura*, ou lorsqu'un risque de prédation existe.

En conclusion, bien que notre étude préliminaire nous ait permis de définir un syndrome comportemental au sein de notre population d'individus captifs, ces résultats souffrent de plusieurs limites sur différents aspects. L'utilisation d'un nombre réduits de traits de personnalité ne pourra jamais *a priori* être utilisée pour prédire la personnalité globale des individus, comme on l'a vu avec le trait de persévérance n'intégrant pas le syndrome comportemental. De plus, la caractérisation d'un syndrome comportemental se limite aux conditions et au contexte dans lesquelles ont été effectués les tests de personnalité, de sorte que l'étude dans un contexte donné ne permet pas de prédire l'existence d'un syndrome dans d'autres contextes. Toutefois, eu égard à ces limites expérimentales, la révélation d'un syndrome comportemental au sein de notre population captive de Diamants mandarins nous offre de nouvelles données sur la force et la direction des relations entre traits de personnalité, et nous donne la possibilité d'envisager l'étude d'un nombre réduit de traits en lieu et place d'un plus grand éventail nécessitant une batterie complète de tests. Il est toutefois important de noter que les inférences pouvant en résulter ne peuvent être valides que dans le cadre des traits compris dans l'unité organisationnelle qu'est le syndrome comportemental.

9.2. PERSONNALITÉ ET COMPÉTITION ALIMENTAIRE

Une partie des études existantes sur la personnalité animale a consisté à déterminer ses conséquences en termes d'aptitude phénotypique, afin de comprendre si les personnalités étaient soumises à la sélection naturelle et de tenter d'identifier les pressions de sélection les modelant (Smith & Blumstein 2008). Ainsi, des travaux

conduits sur des populations naturelles de mésanges charbonnières (Dingemanse *et al.* 2004) et d'écureuil roux (Boon *et al.* 2007) ont montré que la relation entre personnalité et aptitude phénotypique était fluctuante à travers les années, donc que les pressions de sélection agissant sur les traits de personnalité n'étaient pas temporellement stables. Les auteurs de ces études ont suggéré que l'intensité de la compétition alimentaire *via* la disponibilité différentielle de nourriture pourrait être un des facteurs écologiques modulant la relation entre personnalité et aptitude phénotypique. Peu d'études s'étaient jusque-là intéressées à l'influence de la personnalité sur l'issue de la compétition par interférence (Fox *et al.* 2009) ou par exploitation (Kurvers *et al.* 2010a). Notre objectif était ainsi d'évaluer dans quelle mesure la personnalité des Diamants mandarins détermine l'issue de la compétition alimentaire par interférence et par exploitation. Dans une première expérience, nous avons montré que les individus proactifs (actifs, explorateurs, enclins à prendre des risques, moins néophobes) devenaient les individus dominants dans l'accès à une source de nourriture unique. A l'inverse, les réactifs avaient de plus grandes chances de terminer subordonnés, donc d'être les derniers à accéder à la mangeoire et d'y passer significativement moins de temps. Ainsi, les individus proactifs seraient positivement sélectionnés dans un contexte de compétition par interférence. Nous noterons que ce résultat est conforme à l'hypothèse du concept du syndrome de rythme de vie (Réale *et al.* 2010), prédisant une relation positive entre un accès préférentiel à la nourriture et la personnalité proactive. Ces hypothèses sont toutefois à prendre avec précaution car certaines études mettent en évidence des relations à l'inverse des prédictions du concept du syndrome du rythme de vie (Réale *et al.* 2010). Par exemple, chez les mésanges de Gambel, ce sont les subordonnées qui sont plus explorateurs que les individus dominants (Fox *et al.* 2009). En contexte de compétition par exploitation, nous avons montré que les individus proactifs (explorateurs) jouissaient d'un succès d'approvisionnement plus faible au cours de jeux producteur-chapardeur. Ce résultat est du à un plus faible taux de découverte des graines de la part des individus proactifs. Ces études, prises ensemble ou séparément,

sont instructives et originales pour plusieurs raisons. D'abord, elles montrent que la compétition alimentaire peut être un facteur écologique liant personnalité et aptitude phénotypique, dans la mesure où le succès alimentaire peut être considéré comme une « devise de conversion » ou un proxy de l'aptitude. Ensuite, elles soulignent l'importance d'étudier les conséquences des personnalités à travers les contextes, étant donné que ces conséquences peuvent être variables et engendrer des pressions de sélection également variables sur l'évolution des personnalités. D'après nos travaux, la sélection agirait positivement sur les individus proactifs lors d'épisodes de compétition par interférence, mais négativement lors d'épisodes de compétition par exploitation, tout du moins chez les Diamants mandarins. Les pressions de sélection fluctuantes à travers les contextes représenteraient un mécanisme potentiellement responsable du maintien de la variation des traits de personnalité. De plus, nos études suggèrent que la constance intra-individuelle de la personnalité représente une contrainte à l'adoption du comportement optimal dans chaque contexte rencontré (figure 1.3.). La direction globale de la sélection naturelle sur les traits de personnalité pourrait être déterminée en évaluant l'importance de chaque type de compétition dans l'écologie de l'espèce étudiée. Ainsi, si les ressources alimentaires sont souvent agrégées dans l'espace, limitant le nombre d'individus pouvant les exploiter simultanément, on peut prédire que les épisodes de compétition par interférence soient plus fréquents que la compétition par exploitation et entraine une sélection globale en faveur des individus proactifs. A l'inverse, si le mode d'approvisionnement principal de l'espèce étudiée consiste à la recherche de graines dispersées sur le sol, il est envisageable que la compétition par exploitation soit plus importante et entraine une sélection positive des individus réactifs. Une approche comparative permettrait de juger de la pertinence de cette prédiction.

En étudiant l'influence de la personnalité sur l'utilisation différentielle des stratégies d'approvisionnement producteur et chapardeur, notre objectif était de déterminer si la variation observée sur les traits de personnalité pouvait être maintenue par le biais de stratégies fréquence-dépendantes. Dans le même temps, les

individus impliqués dans un jeu fréquence-dépendant sont classiquement considérés comme infiniment plastiques et pouvant ajuster leur comportement de manière flexible en fonction des conditions. Or, la personnalité pourrait représenter une contrainte à l'utilisation des tactiques d'approvisionnement et modifier les fréquences des stratégies jouées à l'équilibre. Expérimentalement, quelques études montrent que la personnalité influence l'utilisation différentielle des informations personnelle et sociale chez la bernache nonette (Kurvers *et al.* 2010a,b), la mésange charbonnière (Marchetti & Drent 2000), ou l'épinoche à trois épines (Nomakuchi *et al.* 2009). Dans notre étude sur les Diamants mandarins, les individus explorateurs se révélaient moins efficaces dans la recherche personnelle de graines (tactique producteur) mais nous n'avons pu montrer de différences entre les personnalités dans l'utilisation de la tactique chapardeur. Un artéfact expérimental pourrait être responsable de ce résultat et d'autres études faisant varier les conditions expérimentales, comme la part du découvreur, peuvent être nécessaires pour mettre en évidence une utilisation différentielle des informations personnelle et sociale en fonction de la personnalité. Notre expérience ne nous permet pas non plus d'indiquer clairement si le maintien de la variation sur les traits de personnalité pourrait être favorisé par l'adoption différentielle de tactiques dont les bénéfices dépendent de leurs fréquences dans la population.

En conclusion, nos études sur les relations entre personnalité et stratégies d'approvisionnement en groupe ont permis d'identifier la compétition alimentaire comme potentiellement responsable des liens entre personnalité et aptitude phénotypique. De plus, nos résultats encouragent l'étude transversale de la personnalité à travers plusieurs contextes afin de pouvoir identifier les pressions de sélection globales agissant sur la personnalité pour en prédire l'évolution. Si l'effet différentiel de la personnalité selon les contextes a déjà été documenté (Sih *et al.* 2004a; Duckworth 2006), des techniques d'analyse permettant de prédire l'évolution globale d'un trait de personnalité en fonction de ses conséquences transversales différentes en termes d'aptitude phénotypique à travers les contextes n'ont jamais été

développées. Il y a ici une occasion d'encourager l'étude de la personnalité entre différents contextes, ce qui était originellement l'un des apports du concept de personnalité (Sih *et al.* 2004a), et de développer des techniques d'analyses d'évolution des personnalités en prenant en compte leurs conséquences à travers les contextes à l'aide des différents gradients de sélection y étant mesurés (Hunt *et al.* 2009).

7.3. PERSONNALITÉ ET SÉLECTION SEXUELLE

L'étude simultanée de la personnalité et de la sélection sexuelle revêt un double-intérêt : expliquer la variation couramment observée sur les comportements sexuels (Jennions & Petrie 1997 ; Widemo & Saether 1999) par les variations de personnalité (van Oers *et al.* 2008) ; et déterminer dans quelle mesure la sélection sexuelle peut être responsable du maintien de ces variations de personnalité (Stapley & Keogh 2004 ; Thaker *et al.* 2009).

Notre étude expérimentale a montré que la prise en compte de la personnalité des femelles lors d'expériences de choix du partenaire par association était primordiale pour comprendre une partie de la variation intra-populationnelle mesurée de la sélectivité, des scores de préférence et de leur répétabilité. Notre étude suggère que les femelles de différentes personnalités pourraient ainsi utiliser différentes tactiques d'échantillonnage lors de la recherche d'un partenaire. Ces différences pourraient même faire partie d'un compromis entre vitesse et précision (Chittka *et al.* 2009). Nous prédisons ainsi que les femelles moins actives seraient plus rapides pour réaliser un choix ne correspondant que vaguement à leur préférence sexuelle, alors que les plus actives investiraient plus de temps dans la recherche et l'évaluation d'un partenaire potentiel et seraient ainsi plus susceptibles d'effectuer un choix correspondant à leur préférence sexuelle (figure 9.1.). Toutefois, la vérification de cette hypothèse passe par l'étude *in natura* du comportement sexuel, comme par

exemple la tactique d'échantillonnage, chez des femelles dont la personnalité aurait préalablement été déterminée. Les déplacements des individus, ainsi que leur succès reproducteur devraient pouvoir être suivis au moment de la saison de reproduction. Par exemple, Wilson & McLaughlin (2007) et Farwell & McLaughlin (2009) ont

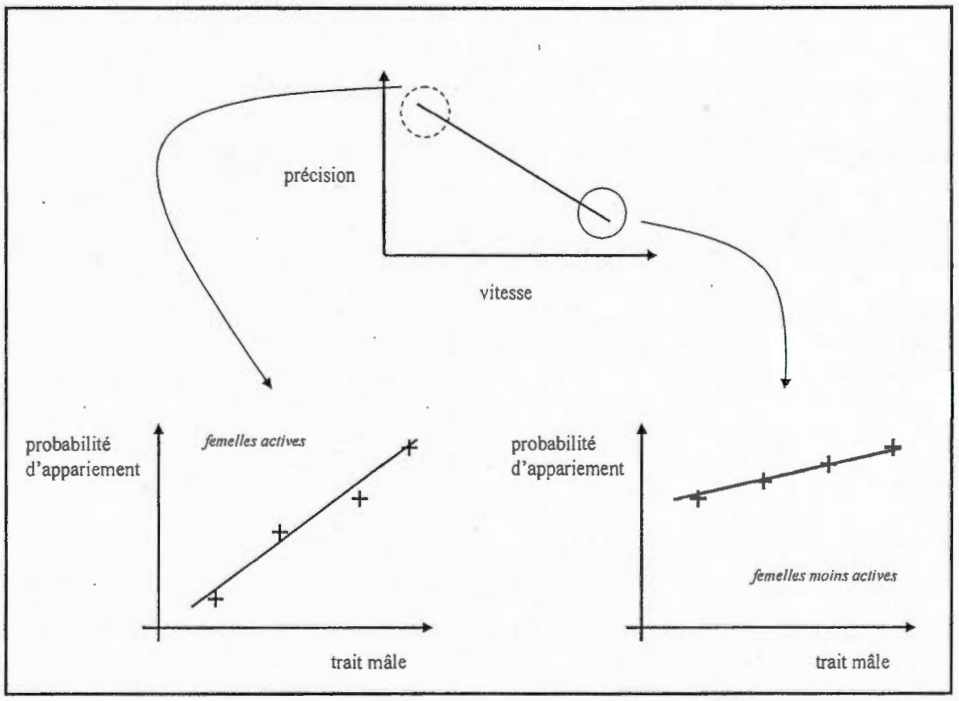

Figure 9.1. Règles de décision hypothétiques lors du choix d'un partenaire en fonction de la personnalité des femelles au sein d'un compromis vitesse/précision. Dans ce schéma, la précision correspond au degré de concordance entre la préférence sexuelle de la femelle et le choix réalisé. On considère ici que les fortes valeurs du trait mâle font l'objet de la préférence de toutes les femelles. La pente plus forte de la probabilité d'appariement des femelles actives indique qu'elles devraient montrer une plus faible probabilité globale d'appariement. En effet, ces femelles devraient montrer un taux de rencontres avec des partenaires potentiels supérieurs, et seraient plus longues pour effectuer un choix mais plus précises, c'est-à-dire plus susceptible de choisir un mâle correspondant à leur préférence. A l'inverse, les femelles moins actives montreraient une probabilité globale d'appariement plus élevée, même avec des mâles ne correspondant que faiblement à leur préférence (faibles valeurs du trait mâle). Ces femelles seraient toutefois plus rapides pour effectuer leur choix.

montré chez l'omble de fontaine (*Salvelinus fontinalis*), que l'intensité des comportements de déplacements dans le cours d'eau et de recherche de proie était positivement reliée aux tendances exploratoires. En contexte de choix d'un partenaire, notre hypothèse est que les femelles les moins actives devraient avoir moins de chance de rencontrer des partenaires du sexe opposé et donc voir se réduire la possibilité de réaliser un choix correspondant à leurs préférences sexuelles. Ce choix sub-optimal pourrait avoir pour effet de diminuer le succès reproducteur desdites femelles. En plus de suggérer que la variation intra-populationnelle au niveau des comportements sexuels soit liée aux variations de personnalité, notre étude montre que la sélectivité et la préférence mesurées dépendent de la personnalité des femelles. Ces relations sont susceptibles de biaiser les résultats des tests de choix du partenaire en fonction de la personnalité moyenne des femelles de l'échantillon étudié, et ainsi d'influencer les interprétations en terme de pressions de sélection sexuelle. Ces conséquences prennent un sens particulier chez une espèce comme le Diamant mandarin pour laquelle l'objet véritable de la préférence des femelles est largement débattu (Collins & ten Cate 1996). Il est envisageable que les résultats contrastés obtenus entre les études trouvent leur cause dans l'influence de la personnalité moyenne des femelles de l'échantillon, surtout pour les études de choix du partenaire où les tailles d'échantillon sont traditionnellement faibles.

Notre revue critique de la littérature a permis de mettre l'accent sur une partie négligée de l'étude de la personnalité, soit ses liens avec la sélection sexuelle, en mettant en évidence les bénéfices liés à leur étude conjointe. Nous avons ainsi proposé que la sélection sexuelle puisse contribuer au maintien de la variation sur les traits de personnalité en prenant comme exemple des études conduites chez des espèces de lézard chez qui les tactiques alternatives de reproduction sont liées à des personnalités distinctes (Stapley & Keogh 2004 ; Thaker *et al.* 2009). De plus, l'étude conjointe de la personnalité et des tactiques alternatives de reproduction pourrait contribuer à la compréhension des mécanismes proximaux à l'origine de la

personnalité, et permettre d'aborder ce concept chez une catégorie différente d'organismes que ceux traditionnellement étudiés. Toutefois, le rôle de la sélection inter-sexuelle sur le maintien des personnalités reste peu étudié. Pourtant, l'étude des stratégies d'appariement en fonction de la personnalité des partenaires possède le potentiel de mettre évidence un mécanisme simple, l'homogamie positive, à l'origine d'une sélection diversifiante sur la personnalité (Groothuis & Carere 2005).

Bien que ce sujet reste un des thèmes les moins étudiés en lien avec la personnalité, de plus en plus d'études montrent une influence significative de la personnalité sur les comportements sexuels des organismes (Reaney & Backwell 2007 ; van Oers *et al.* 2008). Godin & Dugatkin (1996) ont même proposé que la personnalité puisse être l'objet principal du choix des femelles guppies, au-delà de la morphologie des mâles. La théorie de la sélection inter-sexuelle fait l'objet depuis une douzaine d'année d'interrogations croissantes à propos de la variation dont font preuve les organismes dans leurs comportements sexuels (Jennions & Petrie 1997). Le choix du partenaire, *via* la préférence des femelles est considéré comme une pression de sélection majeure dans l'évolution des caractères sexuels secondaires (Danchin & Cézilly 2005). Pourtant, les comportements des femelles montrent au niveau populationnel une variation certaine. Si cette variation a pu, à l'instar de la personnalité, être considérée pour un temps comme de la variation résiduelle autour d'une moyenne adaptative, ses causes et ses conséquences sont aujourd'hui l'objet de l'attention d'études tentant de comprendre ses origines et ses implications dans la théorie de la sélection sexuelle (Widemo & Saether 1999 ; Chaine & Lyon 2008). Ces perspectives offrent une occasion, déjà illustrée par quelques études empiriques (Godin & Dugatkin 1996 ; van Oers *et al.* 2008), d'associer personnalité et sélection inter-sexuelle afin de déterminer dans quelle mesure la variation intra-populationnelle de personnalité pourrait rendre compte de la variation pour l'instant inexpliquée de certains comportements sexuels, comme la sélectivité, la préférence ou la réceptivité des femelles (Jennions & Petrie 1997).

En conclusion, le concept de personnalité apporte des perspectives nouvelles en écologie comportementale en ce qu'il fournit l'opportunité d'expliquer la variation observée sur des stratégies biodémographiques et propose d'envisager son évolution à travers les différents contextes de vie d'un organisme (Sih *et al.* 2004b). De plus, l'intérêt de l'étude de la personnalité est historiquement basé sur l'explication de la variation dont ses traits font preuve, et une partie des études lui étant consacrée permet de déterminer si la personnalité peut évoluer par sélection naturelle ou sexuelle. Les thèmes abordés au cours de cette thèse s'inscrivent dans ces perspectives originales en abordant l'évolution de la personnalité à travers différents contextes (la compétition alimentaire et la sélection sexuelle). Aussi, nous avons pu mettre en évidence l'influence de la personnalité sur certains comportements alimentaires et sexuels des organismes, identifiant ainsi de nouvelles causes permettant de comprendre quelles sont les pressions de sélection modelant à la fois l'évolution de la personnalité et celle des comportements alimentaires et sexuels. Ces résultats ne représentent toutefois que l'amorce de projets à la fois plus spécifiques et plus globaux faisant de la personnalité un facteur pertinent de l'étude des comportements alimentaires et sexuels, et de l'analyse de ces comportements une voie prometteuse dans l'étude de l'évolution de la personnalité.

BIBLIOGRAPHIE

Adkins-Regan, E. et Robinson, T. M. 1993. Sex differences in aggressive behavior in zebra finches (*Poephila guttata*). *J. Comp. Psychol.*, 107, 223-229.

Adriaenssens, B. et Johnsson, J. I. 2009. Personality and life-history productivity : consistent or variable association? *Trends Ecol. Evol.*, 24, 179-180.

Adriaenssens, B. et Johnsson, J. I. 2011. Shy trout grow faster: exploring the links between personality and fitness-related traits in the wild. *Behav. Ecol.*, 22, 135-143.

Alonzo, S. H. 2008. Female mate choice copying affects sexual selection in wild populations of the ocellated wrasse. *Anim. Behav.*, 75, 1715-1723.

Álvarez, D. et Bell, A. M. 2007. Sticklebacks from streams are more bold than sticklebacks from ponds. *Behav. Proc.*, 76, 215-217.

Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton.

Andersson, M. et Simmons, L. W. 2006. Sexual selection and mate choice. *Trends Ecol. Evol.*, 21, 296-302.

Arens, J. R. et Cooper, S. J. 2005. Metabolic and ventilatory acclimatization to cold stress in House Sparrows (*Passer domesticus*). *Physiol. Biochem. Zool.*, *78*, 579-589.

Ashton, M. C. et Lee, K. 2007. Empirical, theoretical, and practical advantages of the HEXACO model of personality structure. *Pers. Soc. Psychol.*, 11, 150-166.

Bailey, N. W. 2008. Love will tear you apart: different components of female choice exert contrasting selection pressures on male field crickets. *Behav. Ecol.*, 19, 960-966.

Barnard, C. J. 1984. *Producers and scrounger: strategies of exploitation and parasitism*, Chapman et Hall.

Barnard, C. J. et Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.*, 29, 543-555.

Bateson, M. et Healy, S. D. 2005. Comparative evaluation and its implications for mate choice. *Trends Ecol. Evol.*, 20, 679-664.

Beauchamp G. 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour*. 137:301-314.

Beauchamp, G. 2001. Consistency and flexibility in the scrounging behaviour of zebra finches. *Can. J. Zool.*, 79, 540-544.

Beauchamp, G. 2006. Phenotypic correlates of scrounging behavior in zebra finches: role of foraging efficiency and dominance. *Ethology*, 112, 873-878.

Bell, A. M. 2007. Future directions in behavioural syndromes research. *Proc. R. Soc. Lond. B*, 274, 755-761.

Bell, A. M. et Stamps, J. A. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Anim. Behav.*, 68, 1339-1348.

Bell, A. M. et Sih, A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol. Lett.*, 10, 828-834.

Bell, A. M., Hankison, S. J. et Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Anim. Behav.*, 77, 771-783.

Benjamini, Y. et Hochberg, Y. 1995. Controlling the false discovery rate – a practical and powerful approach to multiple testing. *J. R. Stat. Soc. B*, 57, 289-300.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. et Maier, E. J. 1996. Ultraviolet vision and mate choice in zebra finches. *Nature*, 380, 433-435.

Bergmüller, R. 2010. Animal personality and behavioural syndromes. In: *Animal behaviour – Evolution and mechanisms* (Ed. by Kappeler, P.) pp. 587-621. Heidelberg: Springer.

Birkhead, T. R., Fletcher, F. et Pellatt, E. J. 1998. Sexual selection in the zebra finch *Taeniopygia guttata*: condition, sex traits and immune capacity. *Behav. Ecol. Sociobiol.*, 44, 179-191.

Biro, P. A. et Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.*, 23, 361-368.

Biro, P. A. et Booth, D. J. 2009. Extreme boldness precedes starvation mortality in six-lined trumpeter (*Pelates sexlineatus*). *Hydrobiologia*, 635, 395-398.

Biro, P. A. et Dingemanse, N. J. 2009. Sampling bias resulting from animal personality. *Trends Ecol. Evol.*, 24, 66-67.

Biro, P. A., Abrahams, M. V., Post, J. R. et Parkinson, E. A. 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proc. R. Soc. Lond. B*, 271, 2233-2237.

Björklund, M. 1984. The adaptive significance of sexual indistinguishability in birds: a critique of a recent hypothesis. *Oikos* 43, 414-416.

Blanckenhorn, W. V. 1991. Fitness consequences of foraging success in water striders (Gerris remigis; Heteroptera: Gerridae). *Behav. Ecol.*, 2, 46-55.

Blount, J. D., Metcalfe, N. B., Birkhead, T. R. et Surai, P. F. 2003. Carotenoid modulation of immune function and sexual attractiveness in zebra finches. *Science*, 300, 125-127.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. et Forister, M. L. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*, 161, 1-28.

Bolnick, D. I., Snowberg, L. K., Patenia, C., Stutz, W. E., Ingram, T. et Lau, O. L. 2009. Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution*, 63, 2004-2016.

Boogert, N. J., Reader, S. M. et Laland, K. N. 2006. The relation between social rank, neophobia and individual learning in starlings. *Anim. Behav.*, 72, 1229-1239.

Boon, A. K., Réale, D. et Boutin, S. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol. Lett.*, 10, 1094-1104.

Boon, A. K., Réale, D. et Boutin, S. 2008. Personality, habitat use, and their consequences for survival in north American red squirrels *Tamiasciurus hudsonicus*. *Oikos*, 117, 1321-1328.

Both, C., Dingemanse, N. J., Drent, P. J. et Tinbergen, J. M. 2005. Pairs of extreme avian personalities have highest reproductive success. *J. Anim. Ecol.*, 74, 667-674.

Bridge, E. S. et Nisbet, I. C. T. 2004. Wing molt and assortative mating in common terns: a test of the molt-signaling hypothesis. *The Condor* 106, 336-343.

Briffa, M., Rundle, S. D. et Fryer, A. 2008. Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proc. R. Soc. Lond. B*, 275, 1305-1311.

Brodin, T. 2009. Behavioral syndrome over the boundaries of life-carryovers from larvae to adult damselfly. *Behav. Ecol.*, 20, 30-37.

Brooks, R. 1998. The importance of mate copying and cultural inheritance of mating preferences. *Trends Ecol. Evol.*, 13, 45-46.

Brooks, R. et Endler, J. A. 2001. Female guppies agree to differ: phenotypic and genetic variation in mate-choice behavior and the consequences for sexual selection. *Evolution*, 55, 1644-1655.

Brown, C., Burgess, F. et Braithwaite, V. A. 2007. Heritable and experiential effects on boldness in a tropical poeciliid. *Behav. Ecol. Sociobiol.*, 62, 237-243.

Burley, N. T. et Foster, V. S. 2006. Variation in female choice of mates: condition influences selectivity. *Anim. Behav.*, 72, 713-719.

Burley, N., Krantzberg, G. et Radman, P. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. *Anim. Behav.*, 30, 444-455.

Burnham, K. P. et Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Byers, J., Hebets, E. et Podos, J. 2010 Female mate choice based upon male motor performance. *Anim. Behav.* 79, 771-778.

Calkins, J. D. et Burley, N. T. 2003. Mate choice for multiple ornaments in the California quail, *Callipepla californica*. *Anim. Behav.*, 65, 69-81.

Careau, V., Thomas, D., Humphries, M. M. et Réale, D. 2008. Energy metabolism and animal personality. *Oikos*, 117, 641-653.

Careau, V., Réale, D., Humphries, M. M. et Thomas, D. 2010. The pace of life under artificial selection: personality, energy expenditure and longevity are correlated in domestic dogs. *Am. Nat.*, 175, 753-758.

Carere, C. et van Oers, K. 2004. Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. *Physiol. Behav., 82*, 905-912.

Carere, C., Welink, D., Drent, P. J., Koolhaas, J. M. et Groothuis, T. G. G. 2001. Effect of social defeat in a territorial bird (*Parus major*) selected for different coping styles. *Physiol. Behav., 73*, 427-433.

Carere, C., Drent, P. J., Koolhaas, J. M. et Groothuis, T. G. G. 2005. Epigenetic effects on personality traits: early food provisioning and sibling competition. *Behaviour*, 142, 1329-1355.

Carrascal, L. M., Senar, J. C., Mozetich, I., Uribe, F. et Doménech, J. 1998. Interactions among environmental stress, body condition, nutritional status, and dominance in great tits. *Auk*, 115, 727-738.

Carter, A. J., Goldizen, A. W. et Tromp, S. A. 2010. Agamas exhibit behavioral syndromes: bolder males bask and feed more but suffer higher predation. *Behav. Ecol.*, 21, 655-661.

Cézilly, F. 2005. Histoire de l'écologie comportementale. In: *Ecologie comportementale* (ed. by Danchin E., Giraldeau L. –A. et Cézilly F.) pp. 3-26. Dunod, Paris.

Chaine, A. S. et Lyon, B. E. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science*, 319, 459-462.

Chapman, B. B., Morrell, L. J. et Krause, J. 2010. Unpredictability in food supply during early life influences boldness in fish. *Behav. Ecol.*, 21, 501-506.

Chase, I. D., Tovey, C., Spangler-Martin, D. et Manfredonia, M. 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proc Natl. Acad. Sci. U.S.A.*, 99, 5744-5749.

Chittka, L., Skorupski, P. et Raine, N. E. 2009. Speed-accuracy tradeoffs in animal decision making. *Trends Ecol. Evol.*, 24, 400-407.

Clarke, A. et Johnston, N. M. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. *J. Anim. Ecol., 68*, 893-905.

Clobert, J. 1995. Capture-recapture and evolutionary ecology: A difficult wedding? *J. Appl. Stat.*, 22, 989-1008.

Coleman, K. et Wilson, D. S. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.*, 56, 927-936.

Collins, S. A. et ten Cate, C. 1996. Does beak colour affect female preference in zebra finches? *Anim. Behav.*, 52, 105-112.

Colwell, M. A. et Oring, L. W. 1989. Extra-pair mating in the spotted sandpiper: a female mate acquisition tactic. *Anim. Behav.* 38, 675-684.

Cote, J. et Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. Lond. B*, 274, 383-390.

Cote, J., Dreiss, A. et Clobert, J. 2008. Social personality trait and fitness. *Proc. R. Soc. Lond. B*, 275, 2851-2858.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. et Sih, A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proc. R. Soc. Lond. B*, 277, 1571-1579.

Cotton, S., Small, J. et Pomiankowski, A. 2006. Sexual selection and condition-dependent mate preferences. *Curr. Biol.*, 16, R755-R765.

Cristol, D. A. 1992. Food deprivation influences dominance status in dark-eyed juncos, *Junco hyemalis*. *Anim. Behav.*, 43, 117-124.

Dall, S. R. X., Houston, A. I. et McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* 7, 734-739.

Danchin, E. et Cézilly, F. 2005. La sélection sexuelle : un autre processus évolutif. In: *Ecologie comportementale* (ed. by Danchin E., Giraldeau L. –A. et Cézilly F.) pp. 235-298. Dunod, Paris.

Danchin, E. et Cézilly, F. 2008. Sexual selection: another evolutionary process. In *Behavioural Ecology* (Ed. by E. Danchin; L.–A. Giraldeau et F. Cézilly) pp. 363-426. Oxford University Press.

Danchin, E., Giraldeau, L. –A., Valone, T. J. & Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. *Science*, 305, 487-491.

David, M., Auclair, Y. et Cézilly, F. 2011a. Personality predicts social dominance in the zebra finch, *Taeniopygia guttata*, in a feeding context. *Anim. Behav.*, 81, 219-224.

David, M., Cézilly, F. et Giraldeau, L. –A. 2011b. Personality affects zebra finch feeding success in a producer-scrounger game. *Anim. Behav.*, 82, 61-67.

David, M. et Cézilly, F. sous presse. Personality can confound common measures of mate-choice. *PLoS ONE.*

David, M. et Giraldeau, L. –A. 2012. Zebra finches in poor condition produce more and consume more food in a producer-scrounger game. *Behav. Ecol.*, 23, 174-180.

David, M., Auclair, Y., Dechaume-Moncharmont, F. X. et Cézilly, F. sous presse. Handling stress does not reflect personality in female zebra finches. *J. Comp. Psychol.*

Dewan, A. K., Maruska, K. P. et Tricas, T. C. 2008. Arginine vasotocin neuronal phenotypes among congeneric territorial and shoaling reef butterflyfishes:

species, sex and reproductive season comparisons. *J. Neuroendocrinol.*, 20, 1382-1394.

DeWitt, T. J., Sih, A. et Wilson, D. S. 1998. Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.*, 13, 77-81.

Dijkstra, P. D., van Dijk, S., Groothuis, T. G. G., Pierotti, M. E. R. et Seehausen, O. 2009. Behavioral dominance between female color morphs of a Lake Victoria cichlid fish. *Behav. Ecol.*, 20, 593-600.

Dingemanse, N. J. et de Goede, P. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav. Ecol.*, 15, 1023-1030.

Dingemanse, N. J. et Réale, D. 2005. Natural selection and animal personality. *Behaviour*, 142, 1159-1184.

Dingemanse, N. J. et Wolf, M. 2010. Recent models for adaptive personality differences: a review. *Phil. Trans. R. Soc. Lond. B*, 365, 3947-3958.

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K. et van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.*, 64, 929-938.

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L. et Drent, P. J. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proc. R. Soc. Lond. B*, 270, 741-747.

Dingemanse, N. J., Both, C., Drent, P. J. et Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proc. R. Soc. Lond. B*, 271, 847-852.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. et Dawnay, N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined sticklebacks. *J. Anim. Ecol.*, 76, 1128-1138.

Dingemanse, N. J., Kazem, A. J. N., Réale, D. et Wright, J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.*, 25, 81-89.

Dochtermann, N. A. et Jenkins, S. H. 2007. Behavioural syndromes in Merriam's kangaroo rats (*Dipodomys merriami*): a test of competing hypotheses. *Proc. R. Soc. Lond. B*, 274, 2343-2349.

Dolan, R. J. 2002. Emotion, cognition and behavior. *Science*, 298, 1191-1194.

Doucet, S. M., Yezerinac, S. M. et Montgomerie, R. 2004. Do female zebra finches (*Taeniopygia guttata*) copy each other's mate preferences? *Can. J. Zool.*, 82, 1-7.

Drent, P. J., van Oers, K. et van Noordwijk, A. J. 2003. Realized heritability of personalities in the great tit (*Parus major*). *Proc. R. Soc. Lond. B*, 270, 45-51.

Drullion, D. et Dubois, F. 2008. Mate-choice copying by female zebra finches, *Taeniopygia guttata*: what happens when model females provide inconsistent information? *Behav. Ecol. Sociobiol.*, 63, 269-276.

Dubois, F. et Giraldeau, L. –A. 2004. Reduced resource defence in an uncertain world: an experimental test using captive nutmeg mannikins. *Anim. Behav.*, 68, 21-25.

Duckworth, R. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behav. Ecol.*, 17, 1011-1019.

Dugatkin, L. A. et Godin, J. –G. J. 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behav. Ecol.*, 4, 289-292.

Dyer, J. R. G., Croft, D. P., Morrell, L. J. et Krause, J. 2009. Shoal composition determines foraging success in the guppy. *Behav. Ecol.*, 20, 165-171.

Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethol. Sociobiol.*, 16, 257-333.

Endler, J. A. 1986a. The newer synthesis? Some conceptual problems in evolutionary biology. *Oxf. Sur. Evol. Biol.*, 3, 224-243.

Endler, J. A. 1986b. *Natural selection in the wild.* Princeton University Press, Princeton.

Evans, J., Boudreau, K. et Hyman, J. 2010. Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, 116, 588-595.

Farwell, M. et McLaughlin, R. L. 2009. Alternative foraging tactics and risk-taking in brook charr (*Salvelinus fontinalis*). *Behav. Ecol.*, 20, 913-921.

Fernández-Juricic, E. et Beauchamp, G. 2008. An experimental analysis of spatial position effects on foraging and vigilance in brown-headed cowbird flocks. *Ethology*, 114, 105-114.

Fidler, A. E., van Oers, K., Drent, P. J., Kuhn, S., Mueller, J. C. et Kempenaers, B. 2007. *Drd4* gene polymorphisms are associated with personality variation in a passerine bird. *Proc. R. Soc. Lond. B*, 274, 1685-1691.

Figueredo, A. J., Cox, R. L. et Rhine, R. J. 1995. A generalizability analysis of subjective personality assessments in the Stumptail macaque and the Zebra finch. *Multivar. Behav. Res.*, 30, 167-197.

Fisher, M. O., Nager, R. G. et Monaghan, P. 2006. Compensatory growth impairs adult cognitive performance. *PloS Biol.*, 4(8), e251.

Forsgren, E., Karlsson, A. et Kvanermo, C. 1996. Female sand gobies gain direct benefits by choosing males with eggs in their nests. *Behav. Ecol. Sociobiol.*, 39, 91-96.

Forstmeier, W. 2004. Female resistance to male seduction in zebra finches. *Anim. Behav.*, 68, 1005-1015.

Forstmeier, W. 2007. Do individual females differ intrinsically in their propensity to engage in extra-pair copulations? *PLoS ONE*, 2(9), e952.

Forstmeier, W. et Birkhead, T. R. 2004. Repeatability of mate choice in the zebra finch: consistency within and between females. *Anim. Behav.*, 68, 1017-1028.

Forstmeier, W., Coltman, D. W. et Birkhead, T. R. 2004. Maternal effects influence the sexual behaviour of sons and daughters in the zebra finch. *Evolution*, 58, 2574-2583.

Fox, R. A., Ladage, L. D., Roth II, T. C. et Pravosudov, V. V. 2009. Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Anim. Behav.*, 77, 1441-1448.

Frommen, J. G., Rahn, A. K., Schroth, S. H., Waltschyk, N. et Bakker, T. C. M. 2009. Mate-choice copying when both sexes face high costs of reproduction. *Evol. Ecol.*, 23, 435-446.

Fucikova, E., Drent, P. J., Smits, N. et van Oers, K. 2009. Handling stress as a measurement of personality in great tit nestlings (*Parus major*). *Ethology*, 115, 366-374.

Galef, B. G. et White, D. J. 1998. Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*. *Anim. Behav.*, 55, 545-552.

Galef, B. G., Lim, T. C. W. et Gilbert, G. S. 2008. Evidence of mate choice copying in Norway rats, *Rattus norvegicus*. *Anim. Behav.*, 75, 1117-1123.

Garamszegi, L. Z. 2011. Information-theoretic approaches to statistical analysis in behavioural ecology: an introduction. *Behav. Ecol. Sociobiol.*, 65, 1-11.

Garamszegi, L. Z., Eens, M. et Török, J. 2008. Birds reveal their personality when singing. *PLoS ONE*, 3(7), e2647.

Garamszegi, L. Z., Eens, M. et Török, J. 2009. Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. *Anim. Behav.*, 77, 803-812.

van Gils, J. A., Schenk, I. W., Bos, O. et Piersma, T. 2003 Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *Am. Nat.*, 161, 777-793.

Giraldeau, L. –A. et Caraco, T. 2000. *Social foraging theory*. Princeton University Press.

Godin, J. –G. J. et Dugatkin, L. A. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proc. Nat. Acad. Sci. U.S.A.*, 93, 10262-10267.

Godin, J. –G. J., Herdman, E. J. E. et Dugatkin, L. A. 2005. Social influences on female mate choice in the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. *Anim. Behav.*, 69, 999-1005.

Gosling, S. D. 1998. Personality dimensions in spotted hyenas (*Crocuta crocuta*). *J. Comp. Psychol.*, 112, 107-118.

Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? *Psychol. Bull.*, 127, 45-86.

Griffith, S. C., Pryke, S. R. et Mariette, M. 2008. Use of nest-boxes by the Zebra Finch (*Taeniopygia guttata*): implications for reproductive success and research. *Emu*, 108, 311-319.

Griggio, M. et Hoi, H. 2010. Only females in poor condition display a clear preference and prefer males with an average badge. *BMC Evol. Biol.*, 10, 261.

Griggio, M., Biard, C., Penn, D. J. et Hoi, H. 2011. Female house sparrows "count on" male genes: experimental evidence for MHC-dependent mate preference in birds. *BMC Evol. Biol.*, 11, 44.

Groothuis, T. G. G. et Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.*, 29, 137-150.

Guillette, L. M., Reddon, A. R., Hurd, P. L. et Sturdy, C. B. 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. *Behav. Proc.*, 82, 265-270.

Hallermann, E. M., McLean, E. et Fleming, I. A. 2007. Effects of growth hormone transgenes on the behavior and welfare of aquacultured fishes: a review identifying research needs. *Appl. Anim. Behav. Sci.*, 104, 265-294.

Harcourt, J. L., Sweetman, G., Johnstone, R. A. et Manica, A. 2009. Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. *Anim. Behav.*, 77, 1501-1505.

Head, M., Hunt, J., Jennions, M. D. et Brooks, R. 2005. The indirect benefits of mating with attractive males outweigh the direct costs. *PLoS Biology*, 3, e33.

Hedrick, A. 1986. Female preferences for male calling bout duration in a field cricket. *Behav. Ecol. Sociobiol.* 19, 73-77.

Hedrick, A. V. 2000. Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proc. R. Soc. Lond. B* 267, 671-675.

Hegyi, G. et Garamszegi, L. Z. 2011. Using information theory as a substitute for stepwise regression in ecology and behavior. *Behav. Ecol. Sociobiol.*, 65, 69-76.

Heisler, I. L., Andersson, M. B., Arnold, S. J., Boake, C. R., Borgia, G., Hausfater, G., Kirkpatrick, M., Lande, R., Maynard Smith, J., O'Donald, P., Thornhill, A. R. et Weissing, F. J. 1987. The evolution of mating preferences and sexually selected traits: group report. In *Sexual Selection: Testing the Alternatives* (Ed. By J.W. Bradbury et M.B. Andersson) pp. 96-118. Chichester: John Wiley.

Helfenstein, F., Wagner, R. H. et Danchin, E. 2003. Functions of courtship feeding in black-legged kittiwakes: natural and sexual selection. *Anim. Behav.* 65, 1027-1033.

Hill, S. E. et Ryan, M. J. 2006. The role of model quality in the mate choice copying behaviour of sailfin mollies. *Biol. Lett.*, 2, 203-205.

Hoeschele, M., Moscicki, M. K., Otter, K. A., van Oort, H., Fort, K. T., Farrell, T. M., Lee, H., Robson, S. W. J. et Sturdy, C. B. 2010. Dominance signalled in an acoustic ornament. *Anim. Behav.* 79, 657-664.

Hohoff, C., Franzen, K. et Sascher, N. 2003. Female choice in a promiscuous wild guinea pig, the yellow-toothed cavy (*Galea musteloides*). *Behav. Ecol. Sociobiol.*, 53, 341-349.

Höjesjö, J., Johnsson, J. et Bohlin, T. 2004. Habitat complexity reduces the growth of aggressive and dominant brown trout (*Salmo trutta*) relative to subordinates. *Behav. Ecol. Sociobiol.*, 56, 286-289.

Holveck, M. –J. et Riebel, K. 2007. Preferred songs predict preferred males: consistency and repeatability of zebra finch females across three test contexts. *Anim. Behav.*, 74, 297-309.

Holveck, M. –J. and Riebel, K. 2009. Low-quality females prefer low-quality males when choosing a mate. *Proc. R. Soc. Lond. B* 277, 153-160.

Hunt, J., Blows, M. W., Zajitschek, F., Jennions, M. D. et Brooks, R. 2007. Reconciling strong stabilizing selection with the maintenance of genetic variation in a natural population of black field crickets (*Teleogryllus commodus*). *Genetics*, 177, 875-880.

Hunt, J., Breuker, C. J., Sadowski, J. A. et Moore, A. J. 2009. Male-male competition, female mate choice and their interaction: determining total sexual selection. *J. Evol. Biol.*, 22, 13-26.

Illius, A. W., Gordon, I. J., Elston, D. A. et Milne, J. D. 1999. Diet selection in goats: a test of intake-rate maximization. *Ecology*, 80, 1008-1018.

Jennions, M. D. et Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.*, 72, 283-327.

van der Jeugd, H. P.et Blaakmeer, K. B. 2001. Teenage love: the importance of trial liaisons, subadult plumage and early pairing in barnacle geese. *Anim. Behav.* 62, 1075-1083.

Johnson, J. C. et Sih, A. 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Anim. Behav.*, 74, 1131-1138.

Jones, A. G. et Ratterman, N. L. 2009. Mate choice and sexual selection: what have we learned since Darwin? *Proc. Natl. Acad. Sci. U.S.A.*, 106, 10001-10008.

Jones, K. A. et Godin, J. –G. J. 2010. Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. *Proc. R. Soc. Lond. B*, 277, 625-632.

Kendal, R. L., Coolen, I. et Laland, K. N. 2009. Adaptive trade-offs in the use of social and personal information. In: Dukas R, Ratcliffe JM (eds) Cognitive ecology II. University of Chicago Press, Chicago, pp 249-271.

Kingston, J. J., Rosenthal, G. G. et Ryan, M. J. 2003. The role of sexual selection in maintaining a colour polymorphism in the pygmy swordtail, *Xiphophorus pygmaeus*. *Anim. Behav.* 65, 735-743.

Knapp, R., Hews, D. K., Thompson, C. W., Ray, L. E. et Moore, M. C. 2003. Environmental and endocrine correlates of tactic switching by nonterritorial male tree lizards (*Urosaurus ornatus*). *Horm. Behav.* 43, 83-92.

Koivula, K., Orell, M. et Rytkoenen, S. 1996. Winter survival and breeding success of dominant and subordinate willow tits, *Parus montanus*. *Ibis*, 138, 624-629.

Kondrashov, A. S. et Shpak, M. 1998. On the origin of species by means of assortative mating. *Proc. R. Soc. Lond. B*, 265, 2273-2278.

Kortet, R. et Hedrick, A. 2005. The scent of dominance: female field crickets use odour to predict the outcome of male competition. *Behav. Ecol. Sociobiol.* 59, 77-83.

Kortet, R. et Hedrick, A. 2007. A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. *Biol. J. Linn. Soc.*, 91, 475-482.

Kotiaho, J. S. et Puurtinen, M. 2007. Mate choice for indirect benefits: scrutiny of the current paradigm. *Funct. Ecol.*, 21, 638-644.

Kralj-Fišer, S., Scheiber, I. B. R., Blejec, A., Moestl, E. et Kotrschal, K. 2007. Individualities in a flock of free-roaming greylag geese: behavioral and physiological consistency over time and across situations. *Horm. Behav.* 51, 239-248.

Krebs, J. R., Erichsen, J. T., Webber, M. I. et Charnov, E. L. 1977. Optimal prey-selection by the Great Tit (*Parus major*). *Anim. Behav.*, 25, 30-38.

Kurvers, R. H. J. M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C. et Prins, H. H. T. 2009. Personality differences explain leadership in barnacle geese. *Anim. Behav.*, 78, 447-453.

Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A. et Ydenberg, R. C. 2010a. The effect of personality on social foraging: shy barnacle geese scrounge more. *Proc. R. Soc. Lond. B*, 277, 601-608.

Kurvers, R. H. J. M., van Oers, K., Nolet, B. A., Jonker, R. M., van Wieren, S. E., Prins, H. H. T. et Ydenberg, R. C. 2010b. Personality predicts the use of social information. *Ecol. Lett.*, 13, 829-837.

Lazarus, J. 1979. Flock size and behaviour in captive red-billed weaverbirds (*Quelea quelea*): implications for social facilitation and the functions of flocking. *Behaviour*, 71, 127-145.

Lehtonen, T. K. et Lindström, K. 2008. Repeatability of mating preferences in the sand goby. *Anim. Behav.*, 75, 55-61.

Lehtonen, T. K. et Lindström, K. 2009. Females decide whether size matters: plastic mate preferences tuned to the intensity of male-male competition. *Behav. Ecol.* 20, 195-199.

Lehtonen, T. K., Wong, B. B. M. et Lindström, K. 2010. Fluctuating mate preference in a marine fish. *Biol. Lett.*, 6, 21-23.

Lemon, W. C. 1991. Fitness consequences of foraging behavior in the zebra finch. *Nature*, 352, 153-155.

Lens, L., Van Dongen, S., Van den Broeck, M., Van Broeckhoven, C. et Dhondt, A. A. 1997. Why female crested tits copulate repeatedly with the same partner: evidence for the mate assessment hypothesis. *Behav. Ecol.* 8, 87-91.

Lessels, C. M. et Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, 104, 116-121.

Luttbeg, B. et Warner, R. R. 1999. Reproductive decision-making by female peacock wrasses: flexible versus fixed behavioral rules in variable environments. *Behavioral Ecology*, 10, 666-674.

Marchetti, C. et Drent, P. J. 2000. Individual differences in the use of social information in foraging by captive great tits. *Anim. Behav.*, 60, 131-140.

Martín, J., López, P. et Cooper Jr, W. E. 2003. When to come out from a refuge: balancing predation risk and foraging opportunities in an alpine lizard. *Ethology* 109, 77-87.

Martin, J. G. A. et Réale, D. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Anim. Behav.*, 75, 309-318.

Martin, P. et Bateson, P. 1993. *Measuring Behaviour: an Introductory Guide*. 2nd edn. Cambridge: Cambridge University Press.

Martin Il, L. B. et Fitzgerald, L. 2005. A taste for novelty in invading house sparrows, *Passer domesticus*. *Behav. Ecol.*, 16, 702-707.

Martins, T. L. F., Roberts, M. L., Giblin, I., Huxham, R. et Evans, M. R. 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Horm. Behav.*, 52, 445-453.

Mathot, K. J. et Giraldeau, L. –A. 2010. Family-related differences in social foraging tactic use in the zebra finch (*Taeniopygia guttata*). *Behav. Ecol. Sociobiol.*, 64, 1805-1811.

Mathot, K. J., Godde, S., Careau, V., Thomas, D. W. et Giraldeau, L. –A. 2009. Testing dynamic variance-sensitive foraging using individual differences in basal metabolic rates of Zebra Finches. *Oikos*, 118, 545-552.

Maynard-Smith, J. 1982. *Evolution and the theory of games.* Cambridge University Press, Cambridge.

McCrae, R. R., Costa Jr, P. T., Del Pilar, G. H., Rolland, J. –P. et Parker, W. D. 1998. Cross-cultural assessment of the five-factor model. *J. Cross. Cult. Psychol.*, 29, 171-188.

McNab, B. K. 2002. *The physiological ecology of vertebrates: a view from energetics*. Ithaca, NY: Cornell University Press.

Mennill, D. J., Ramsay, S. M., Boag, P. T. et Ratcliffe, L. M. 2004. Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. *Behav. Ecol.*, 15, 757-765.

Merilä, J., Kruuk, L. E. B. et Sheldon, B. C. 2001. Natural selection on the genetical component of variance in body condition in a wild bird population. *J. Evol. Biol.*, 14, 918-929.

Mery, F., Varela, S. A. M., Danchin, E., Blanchet, S., Parejo, D., Coolen, I. et Wagner, R. H. 2009. Public versus personal information for mate copying in an invertebrate. *Curr. Biol.*, 19, 730-734.

Mettke-Hofmann, C., Winkler, H. et Leisler, B. 2002. The significance of ecological factors for exploration and neophobia in parrots. *Ethology*, 108, 249-272.

Michelena, P., Sibbald, A. M., Erhard, H. W. et McLeod, J. E. 2009. Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behav. Ecol.*, 20, 145-152.

Millot, S., Begout, M. –L., Person-Le Ruyet, J., Breuil, G., Di-Poi, C., Fievet, J., Pineau, P., Roue, M. et Severe, A. 2008. Feed demand behavior in sea bass juveniles: effects on individual specific growth rate variation and health (inter-individual and inter-group variation). *Aquaculture*, 274, 87-95.

Milner, R. N. C., Detto, T., Jennions, M. D. et Backwell, P. R. Y. 2010. Experimental evidence for a seasonal shift in strength of a female mating preference. *Behav. Ecol.*, 21, 311-316.

Møller, A. P. et Alatalo, R. V. 1999. Good-genes effects in sexual selection. *Proc. R. Soc. B*, 266, 85-91.

Møller, A. P., Nielsen, J. T. et Garamszegi, L. Z. 2008. Risk-taking by singing males. *Behav. Ecol.*, 19, 41-53.

Montiglio, P. O., Garant, D., Thomas, D. et Réale, D. 2010. Individual variation in temporal activity patterns in open-field tests. *Anim. Behav.*, 80, 905-912.

Moore, A. J., Gowaty, P. A., Wallin, W. G. et Moore, P. J. 2001. Sexual conflict and the evolution of female mate choice and male social dominance. *Proc. R. Soc. Lond. B.*, 268, 517-523.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, 100, 403-405.

Morand-Ferron, J., Varennes, E et Giraldeau, L. –A. 2010. Individual differences in plasticity and sampling when playing behavioural games. *Proc. R. Soc. Lond. B*, 278, 1223-1230.

Mota Silva, P. I., Martins, C. I. M., Engrola, S., Marino, G., Øverli, Ø. et Conceição, L. E. C. 2010. Individual differences in cortisol levels and behaviour of Senegalese sole (*Solea senegalensis*) juveniles: evidence for coping styles. *Appl. Anim. Behav. Sci.* 124, 75-81.

Naguib, M., Kazek, A., Schaper, S. V., van Oers, K. et Visser, M E. 2010. Singing activity reveals personality traits in great tits. *Ethology*, 116, 763-769.

Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behav. Ecol.*, 15, 1044-1045.

Nakagawa, S. et Cuthill, I. C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.*, 82, 591-605.

Nakagawa, S. et Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol. Rev.*, 85, 935-956.

Narraway, C., Hunt, J., Wedell, N. et Hosken, D. J. 2010. Genotype-by-environment interactions for female preference. *J. Evol. Biol.*, 23, 2550-2557.

Nielsen, B. L. 1999. On the interpretation of feeding behaviour measures and the use of feeding rate as an indicator of social constraint. *Appl. Anim. Behav. Sci.*, 63, 79-91.

Nomakuchi, S., Park, P. J. et Bell, M. A. 2009. Correlation between exploration activity and use of social information in three-spined sticklebacks. *Behav. Ecol.*, 20, 340-345.

van Oers, K., Drent, P. J., de Jong, G. et van Noordwijk, A. J. 2004a. Additive and nonadditive genetic variation in avian personality traits. *Heredity*, 93, 496-503.

van Oers, K., de Jong, G. , Drent, P. J. et van Noordwijk, A. J. 2004b. A genetic analysis of avian personality traits: correlated, response to artificial selection. *Behav. Genet.*, 34, 611-619.

van Oers, K., Drent, P. J., de Goede, P. et van Noordwijk, A. J. 2004c. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc. R. Soc. Lond. B*, 271, 65-73.

van Oers, K., Drent, P. J., Dingemanse, N. J. et Kempenaers, B. 2008. Personality is associated with extrapair paternity in great tits, *Parus major*. *Anim. Behav.*, 76, 555-563.

Oliveira, R. F., Ros, A. F. H. & Gonçalves, D. M. 2005. Intra-sexual variation in mal reproduction in teleost fish: a comparative approach. *Horm. Behav.*, 48, 430-439.

Oliveira, R. F., Taborsky, M. et Brockmann, H. J. 2008. *Alternative reproductive tactics – an integrative approach*. Cambridge University Press, Cambridge.

Ophir, A. G. et Galef, B. G. 2004. Sexual experience can affect use of public information in mate choice. *Anim. Behav.*, 68, 1221-1227.

Owens, I. P. F. 2006. Where is behavioural ecology going? *Trends Ecol. Evol.*, 21, 356-361.

Owens, I. P. F. et Hartley, I. R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. Lond. B.*, 265, 397-407.

Parker, G. A. 1983. Arms races in evolution-an ESS to the opponent-independent costs game. *J. Theor. Biol.*, 101, 619-648.

Paunonen, S.V. et Ashton, M.C. 2001. Big five factors and facets and the prediction of behavior. *J. Pers. Soc. Psychol.*, 81, 524-539.

Paunonen, S. V., Haddock, G., Forsterling, F. et Keinonen, M. 2003. Broad versus narrow personality measures and the prediction of behaviour across cultures. *Eur. J. Pers.*, 17, 413-433.

Pearn, S. M., Bennett, A. T. D. et Cuthill, I. C. 2001. Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar, *Melopsittacus undulatus*. *Proc. R. Soc. Lond. B*, 268, 2273-2279.

Pearn, S. M., Bennett, A. T. D. et Cuthill, I. C. 2001. Ultraviolet vision, fluorescence

and mate choice in a parrot, the budgerigar, *Melopsittacus undulatus*. *Proc. R. Soc. Lond. B*, 268, 2273-2279.

Pervin, L. et John, O. P. 1997. *Personality: Theory and research* (7th ed.). New York: Wiley.

Pryke, S. R. 2009. Is red an innate or learned signal of aggression and intimidation? *Anim. Behav.*, 78, 393-398.

Pryke, S. R. et Griffith, S. C. 2006. Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proc. R. Soc. Lond. B*, 273, 949-957.

Quinn, J. L. et Cresswell, W. 2005. Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour*, 142, 1377-1402.

Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A. et Sheldon, B. C. 2009. Heterogeneous selection on a heritable temperament trait in a variable environment. *J. Anim. Ecol.*, 78, 1203-1215.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Radwan, J. 2008. Maintenance of genetic variation in sexual ornaments: a review of the mechanisms. *Genetica*, 134, 113-127.

Rammstedt, B. et Schupp, J. 2008. Only the congruent survive – Personality similarities in couples. *Pers. Ind. Diff.*, 45, 533-535.

Rands, S. A., Cowlishaw, G., Pettifor, R. A., Rowcliffe, J. M. et Johnstone, R. A. 2003. Spontaneous emergence of leaders and followers in foraging pairs. *Nature*, 423, 432-434.

Réale, D. et Festa-Bianchet, M. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Anim. Behav.*, 65, 463-470.

Réale, D., Gallant, B. Y., Leblanc, M. et Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life-history. *Anim. Behav.*, 60, 589-597.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. et Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.*, 82, 291-318.

Réale, D., Martin, J., Coltman, D. W., Poissant, J. et Festa-Bianchet, M. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.*, 22, 1599-1607.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V. et Montiglio, P. – O. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil. Trans. R. Soc. Lond. B*, 365, 4051-4063.

Reaney, L. T. et Backwell, P. R. Y. 2007. Risk-taking behavior predicts aggression and mating success in a fiddler crab. *Behav. Ecol.*, 18, 521-525.

Reinhold, K., Reinhold, K. et Jacoby, K. J. 2002. Dissecting the repeatability of female choice in the grasshopper *Chorthippus biguttulus*. *Anim. Behav.*, 64, 245-250.

Ricklefs, R. E. et Wikelski, M. 2002. The physiology/life-history nexus. *Trends Ecol. Evol.*, 17, 462-468.

Rios-Cardenas, O., Scarlett Tudor, M. et Morris, M. R. 2007. Female preference variation has implications for the maintenance of an alternative mating strategy in a swordtail fish. *Anim. Behav.*, 74, 633-640.

Ritchie, M. E. 1990. Optimal foraging and fitness in Columbian ground squirrels. *Oecologia*, 82, 56-67.

Ritchie, M. G., Hamill, R. M., Graves, J. A., Magurran, A. E., Webb, S. A. et Macías Garcia, C. 2007 Sex and differentiation: population genetic divergence and sexual dimorphism in Mexican goodeid fish. *J. Evol. Biol.*, 20, 2048-2055.

Ritschard, M., Riebel, K. et Brumm, H. 2010. Female zebra finches prefer high-amplitude song. *Anim. Behav.*, 79, 877-883.

Rønning, B., Moe, B. et Bech, C. 2005. Long-term repeatability makes basal metabolic rate a likely heritable trait in the zebra finch *Taeniopygia guttata. J. Exp. Biol.*, 208, 4663-4669.

Rutstein, A. N., Brazill-Boast, J. et Griffith, S. C. 2007. Evaluating mate choice in the zebra finch. *Anim. Behav.*, 74, 1277-1284.

Schamber, J. L., Esler, D. et Flint, P. L. 2009. Evaluating the validity of using unverified indices of body condition. *J. Avian Biol.*, 40, 49-56.

Scheid, C. et Noë, R. 2010. The performance of rooks in a cooperative task depends on their temperament. *Anim. Cogn.*, 13, 545-553.

Schubert, K. A., Mennill, D. J., Ramsay, S. M., Otter, K. A., Ratcliffe, L. M. et Kraus, C. 2008. Between-year survival and rank transition in male Black-capped Chickadees (*Poecile atricapillus*): A multisite modelling approach. *Auk*, 125, 629-636.

Schuett, W. 2008. *Sexual selection and personality in zebra finches (Taeniopygia guttata)*. Thèse de doctorat, Université d'Exeter, Penryn, UK.

Schuett, W. et Dall, S. R. X. 2009. Sex differences, social context and personality in zebra finches, *Taeniopygia guttata. Anim. Behav.*, 77, 1041-1050.

Schuett, W., Tregenza, T. et Dall, S. R. X. 2010. Sexual selection and animal personality. *Biol. Rev.*, 85, 217-246.

Schuett, W., Dall, S. R. X. et Royle, N. J. 2011. Pairs of zebra finches with similar 'personalities' make better parents. *Anim. Behav.*, 81, 609-618.

Schuett, W., Godin, J. –G. J. et Dall, S. R. X. sous presse. Do female zebra finches, *Taeniopygia guttata*, choose their mates based on their "personality"?. *Ethology*.

Schwartz, M. K., Boness, D. J., Schaeff, C. M., Majluf, P., Perry, E. A. et Fleischer, R. C. 1999. Female-solicited extrapair matings in Humboldt penguins fail to produce extrapair fertilizations. *Behav. Ecol.*, 10, 242-250.

Seferta, A., Guay, P. -J., Marzinotto, E. et Lefèbvre, L. 2001. Learning differences between feral pigeons and Zenaida doves: The role of neophobia and human proximity. *Ethology*, 107, 281-293.

Semsar, K., Kandel, F. L. M. et Godwin, J. 2001. Manipulations of the AVT system shift social status and related courtship and aggressive behavior in the bluehead wrasse. *Horm. Behav.*, 40, 21-31.

Shackleton, M. A., Jennions, M. D. et Hunt, J. 2005. Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests. *Behav. Ecol. Sociobiol.*, 58, 1-8.

Shine, R., Langkilde, T. et Mason, R. T. 2003. The opportunistic serpent: male garter snakes adjust courtship tactics to mating opportunities. *Behaviour*, 140, 1509-1526.

Sih, A. et Bell, A. M. 2008. Insights for behavioral ecology from behavioral syndromes. *Adv. Stud. Behav.*, 38, 227-281.

Sih, A., Kats, L. B. et Maurer, E. F. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Anim. Behav.*, 65, 29-44.

Sih, A., Bell, A. et Johnson, J. C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.*, 19, 372-378.

Sih, A., Bell, A. et Johnson, J. C. et Ziemba, R. E. 2004b. Behavioral syndromes: an integrative overview. *Q. Rev. Biol.*, 79, 241-277.

Sinervo, B. et Lively, C. M. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, 380, 240-243.

Sinn, D. L., Apiolaza, L. A. et Moltschaniwskyj, N. A. 2006. Heritability and fitness-related consequences of squid personality traits. *J. Evol. Biol.*, 19, 1437-1447.

Smith, B. R. et Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behav. Ecol.*, 19, 448-455.

Sokal, R. R. et Rohlf, F. J. 1995. *Biometry, the principles and practice of statistics in biological research.* 3rd edn. Freeman et Company, New York.

Soldz, S. et Vaillant, G. E. 1999. The big five personality traits and the life course: a 45-year longitudinal study. *J. Res. Pers.*, 33, 208-232.

Soler, M., Soler, J. J., Møller, A. P., Moreno, J. et Lindén, M. 1996. The functional significance of sexual display: stone carrying in the black wheatear. *Anim. Behav.*, 51, 247-254.

Sorci, G. et Cézilly, F. 2005. Interactions durables. In: *Ecologie comportementale* (ed. by Danchin E., Giraldeau L. –A. et Cézilly F.) pp. 475-501. Dunod, Paris.

Spencer, K. A. et Verhulst, S. 2007. Delayed behavioral effects of postnatal exposure to corticosterone in the zebra finch (*Taeniopygia guttata*). *Horm. Behav.*, 51, 273-280.

Spoon, T. R., Millam, J. R. et Owings, D. H. 2006. The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Anim. Behav.*, 71, 315-326.

Spoon, T. R., Millam, J. R. et Owings, D. H. 2007. Behavioural compatibility, extrapair copulation and mate switching in a socially monogamous parrot. *Anim. Behav.*, 73, 815-824.

Srivastava, S., John, O. P., Gosling, S. D. et Potter, J. 2003. Development of personality in early and middle adulthood: set like plaster or persistent change? *Pers. Soc. Psychol.*, 84, 1041-1053.

Stamps, J. A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol. Lett.*, 10, 355-363.

Stapley, J. et Keogh, J. S. 2004. Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards. *Anim. Behav.*, 68, 841-846.

Stirling, D. G., Réale, D. et Roff, D. G. 2002. Selection, structure and the heritability of behaviour. *J. Evol. Biol.*, 15, 277-289.

Strong, A. M. et Sherry, T. W. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *J. Anim. Ecol.*, 69, 883-895.

Sullivan, M. S. 1994. Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Anim. Behav.*, 47, 141-151.

Sundberg, J. 1995. Female yellowhammers (*Emberiza citrinella*) prefer yellower males: a laboratory experiment. *Behav. Ecol. Sociobiol.*, 37, 275-282.

Swaddle, J. P., Cathey, M. G., Correll, M. et Hodkinson, B. P. 2005. Socially transmitted mate preferences in a monogamous bird: a non-genetic mechanism of sexual selection. *Proc. R. Soc. Lond. B*, 272, 1053-1058.

Symonds, M. R. E. et Moussalli, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.*, 65, 13-21.

Ten Eyck, G. R. 2005. Arginine vasotocin activates advertisement calling and movement in the territorial Puerto Rican frog, *Eleutherodactylus coqui*. *Horm. Behav.*, 47, 223-229.

Thaker, M., Lima, S. L. et Hews, D. K. 2009. Alternative antipredator tactics in tree lizard morphs: hormonal and behavioural responses to a predator encounter. *Anim. Behav.*, 77, 395-401.

Tobler, M. et Sandell, M. I. 2007. Yolk testosterone modulates persistence of neophobic responses in adult zebra finches, *Taeniopygia guttata*. *Horm. Behav.*, 52, 640-645.

Uher, J. 2008. Comparative personality research: methodological approaches. *Eur. J. Pers.*, 22, 427-455.

Väisänen, J. et Jensen, P. 2003. Social versus exploration and foraging motivation in young red junglefowl (*Gallus gallus*) and White Leghorn layers. *Appl. Anim. Behav. Sci.*, 84, 139-158.

Vakirtzis, A. et Roberts, S. C. 2010. Nonindependent mate choice in monogamy. *Behav. Ecol.*, 21, 898-901.

Val-Laillet, D., de Passillé, A. M., Rushen, J. et von Keyserlingk, M. A. G. 2008. The concept of social dominance and the social distribution of feeding-related displacements between cows. *Appl. Anim. Behav. Sci.*, 111, 158-172.

Valderrábano-Ibarra, C., Brumon, I. et Drummond, H. 2007. Development of a linear dominance hierarchy in nestling birds. *Anim. Behav.*, 74, 1705-1714.

Verbeek, M. E. M., Drent, P. J. et Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Anim. Behav.*, 48, 1113-1121.

Verbeek, M. E. M., de Goede, P., Drent, P. J. et Wiepkema, P. R. 1999. Individual behavioural characteristics and dominance in aviary groups of great tits. *Behaviour*, 136, 23-48.

Verhoeven, K. J. F., Simonsen, K. L. et McIntyre, L. M. 2005. Implementing false discovery rate control: increasing your power. *Oikos*, 108, 643-647.

Verhulst, S. et Salomons, H. M. 2004. Why fight? Socially dominant jackdaws, *Corvus monedula*, have low fitness. *Anim. Behav.*, 68, 777-783.

de Vries, R. E., Asthon, M. C. et Lee, K. 2009. The six most important personality dimensions and the HEXACO Personality Inventory. *Gedrag et Organisatie*, 22, 232-274.

Vukomanovic, J. et Rodd, F. H. 2007. Size-dependent female mate copying in the guppy (*Poecilia reticulata*): large females are role models but small ones are not. *Ethology*, 113, 579-586.

Waas, J. R. et Wordsworth, A. F. 1999. Female zebra finches prefer symmetrically banded males but only during interactive mate choice tests. *Anim. Behav.*, 57, 1113-1119.

Wade, M. J. et Pruett-Jones, S. G. 1990. Female copying increases the variance in male mating success. *Proc. Natl. Acad. Sci. U.S.A.*, 87,5749-5753.

Wagner, R. H. 1991. The use of extrapair copulations for mate appraisal by razorbills, *Alca torda*. *Behav. Ecol*, 2, 198-203.

Wagner, W. E. 1998. Measuring female mating preferences. *Anim. Behav.*, 55, 1029-1042.

Wagner, W. E. et Basolo, A. L. 2007. The relative importance of different direct benefits in the mate choices of a field cricket. *Evolution*, 61, 617-622.

Walling, C. A., Royle, N. J., Lindström, J. et Metcalfe, N. B. 2010. Do female association preferences predict the likelihood of reproduction? *Behav. Ecol. Sociobiol.*, 64, 541-548.

Ward, A. J. W., Thomas, P., Hart, P. J. B. et Krause, J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav. Ecol. Sociobiol.*, 55, 561-568.

Waynforth, D. 2007. Mate choice copying in humans. *Hum. Nat.*, 18, 264-271.

Westerberg, M., Staffan, F. et Magnhagen, C. 2004. Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. *Anim. Behav.*, 67, 273-279.

While, G. M., Sinn, D. L. et Wapstra, E. 2009. Female aggression predicts mode of paternity acquisition in a social lizard. *Proc. R. Soc. Lond. B*, 276, 2021-2029.

Whiteman, E. A. et Côté, I. M. 2004. Dominance hierarchies in group-living cleaning gobies: causes and foraging consequences. *Anim. Behav.*, 67, 239-247.

Widemo, F. et Saether, S. A. 1999. Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends Ecol. Evol.*, 14, 26-31.

Wiersma, P., Muñoz-Garcia, A., Walker, A. et Williams, J. B. 2007. Tropical birds have a slow pace of life. *Proc. Nat. Acad. Sci. U.S.A.*, 104, 9340-9345.

Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A. et Gwinner, E. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four

stonechat populations from different latitudes. *Proc. R. Soc. Lond. B*, 270, 2383-2388.

Williams, B. R. et Kilgore, D. L. 1992. Ontogenic modification of the hypercapnic ventilatory response in the Zebra finch. *Respir. Physiol.*, 90, 123-134.

Wilson, A. D. M. et Stevens, E. D. 2005. Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, 111, 849-862.

Wilson, A. D. M. et McLaughlin, R. L. 2007. Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Anim. Behav.*, 74, 689-698.

Wilson, A. D. M. et Godin, J. -G. J. 2009. Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behav. Ecol.*, 20, 231-237.

Wilson, A. D. M., Whattam, E. M., Bennett, R., Visanuvimol, L., Lauzon, C. et Bertram, S. M. 2010a. Behavioral correlations across activity, mating, exploration, aggression, and antipredator contexts in the European house cricket, *Acheta domesticus*. *Behav. Ecol. Sociobiol.*, 64, 703-715.

Wilson, A. D. M., Godin, J. –G. J. et Ward, A. J. W. 2010b. Boldness and reproductive fitness correlates in the eastern mosquitofish, *Gambusia holbrooki*. *Ethology*, 116, 96-104.

Wilson, D. S. 1998. Adaptive individual differences within single populations. *Phil. Trans. R. Soc. Lond. B*, 353, 199-205.

Wilson, D. S., Clark, A. B., Coleman, K. et Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends Ecol. Evol.*, 9, 442-446.

Witte, K. 2006. Time spent with a male is a good indicator of mate preference in female zebra finches. *Ethol. Ecol. Evol.*, 18, 195-204.

Witte, K. et Noltemeier, B. 2002. The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). *Behav. Ecol. Sociobiol.*, 52, 194-202.

Wolf, M., van Doorn, G. S., Leimar, O. et Weissing, F. J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447, 581-585.

Woodgate, J. L., Bennett, A. T. D., Leitner, S., Catchpole, C. K. et Buchanan, K. L. 2010. Developmental stress and female mate choice behaviour in the zebra finch. *Anim. Behav.*, 79, 1381-1390.

Zann, R. A. 1996. The zebra finch – a synthesis of field and laboratory studies. Oxford University Press, Oxford.